SOCIAL BEHAVIOUR AND PERSONALITY ASSESSMENT AS A TOOL FOR IMPROVING THE MANAGEMENT OF CHEETAHS (*ACINONYX JUBATUS*) IN CAPTIVITY

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Abstract

The wild cheetah population is rapidly declining, and the captive population is not self-sustaining. This is of great concern for cheetah conservation and the latter might indicate underlying captive welfare concerns. This research measured the behaviour and personality of cheetahs held in zoo exhibits in the UK and beyond, to investigate the effects of social group housing and personality on the behaviour and reproductive success of captive cheetahs.

Behavioural observation indicated that the natural social groupings of wild male cheetahs can be replicated in captivity. Group-housed males displayed frequent affiliative behaviours and few instances of aggression. Females, naturally solitary in the wild, might also be safely housed in groups since overt aggression was seldom recorded. However pacing behaviour, typically associated with poor welfare, was more prevalent in unnatural-type groups. Relatedness appears to be an important factor in captive cheetah social interactions. A new method for correcting indices of association, developed in this research, allowed association indices to be compared for dyads housed in different sized exhibits. Related individuals were observed in proximity more frequently, and displayed higher rates of affiliative interactions, than unrelated individuals. These findings may have welfare implications in the event that captive individuals are separated for management purposes.

Social group housing and personality can affect captive cheetah reproductive success. The personality profiles of individuals in successful breeding pairs were more divergent than those of individuals in unsuccessful pairs. In addition, it appears that zoos housing their cheetahs in social groups that occur in wild populations have better institutional breeding success than those housing their cheetahs in unnatural-type groups. This research uncovers some of the factors which may contribute to the poor reproductive success of the captive cheetah population, and offers recommendations for improvements to current cheetah management practices.

1. Introduction

1.1. Background

One of the goals of the modern zoo is to contribute to the conservation of threatened species by participating in captive breeding programmes, designed to maintain both the genetic diversity and the demographic composition of captive populations (Wedekind, 2002; Ballou *et al*., 2010; Asa *et al*., 2011; Rees, 2011; Hosey *et al*., 2013). Unfortunately, some species have proved difficult to breed in captivity (Snyder *et al*., 1996), which is detrimental to conservation efforts and might indicate underlying welfare concerns. The captive populations of such species are not self-sustaining, and rely on imports from the wild to maintain genetic diversity (Carlstead *et al*., 2000; Bauman *et al*., 2010). Well-known examples include the giant panda (*Ailuropoda melanoleuca*: Powell *et al*., 2008), black rhinoceros (*Diceros bicornis*: Carlstead *et al*., 2000; Carlstead & Brown, 2005) and cheetah (*Acinonyx jubatus*: Carlstead *et al*., 2000; Bauman *et al*., 2010).

The cheetah is best known for its speed and is widely considered to be the fastest land mammal over short distances (Caro, 1994; Sharp, 1997; Durant *et al*., 2008; Quirke *et al*., 2013); an average speed of 103 km hr^{-1} has been recorded for an adult cheetah (Sharp, 1997). Classified as Vulnerable on the IUCN (International Union for Conservation of Nature and Natural Resources) Red List (Durant *et al*., 2008), it is estimated that cheetahs have disappeared from up to 76% of their historic range in Africa, where they remain widely dispersed and occur at low densities (Caro, 1994; Durant *et al*., 2008). Despite the efforts of an international, co-ordinated captive breeding programme, the cheetah has failed to show in captivity the reproductive potential it exhibits in the wild. This is concerning for both cheetah conservation and captive cheetah welfare.

Details of the cheetah's complex social system have been revealed by field observations (Eaton, 1970; Schaller, 1972; Caro & Collins, 1986; Caro, 1994; Marker,

Dickman *et al*., 2003; Durant *et al*., 2004; Gottelli *et al*., 2007). However, social behaviour in captive cheetahs remains an understudied topic. Previous research into the reasons for the poor reproductive success shown by the captive cheetah population has focused on genetics and reproductive physiology (Wildt *et al*., 1983, 1987, 1993; Lindburg *et al*., 1993; Brown *et al*., 1996; Wielebnowski & Brown, 1998; Crosier *et al*., 2007). Whilst several authors identified the need for further research into the behaviour and management of captive cheetahs (Laurenson *et al*., 1992; Caro, 1993; Lindburg *et al*., 1993; Wielebnowski, 1996; Wielebnowski & Brown, 1998; Wielebnowski, Ziegler *et al*., 2002; Crosier *et al*., 2007; Bauman *et al*., 2010), little effort has been made to investigate captive cheetah social behaviour in detail. The cheetah husbandry manual, published by the Association of Zoos and Aquariums (AZA), recommends that male siblings should remain together for life, and that compatible females can be housed in groups (Ziegler-Meeks, 2009). Yet the effects of such management practices have not been quantified in any published research.

The success of captive breeding programmes depends not only on the management of populations or groups, but also on the welfare of individuals. The developing field of animal personality research aims to understand variation among individuals and to assess animal welfare from an individual's perspective (Hill & Broom, 2009; Whitham & Wielebnowski, 2009, 2013; Watters & Powell, 2012). There is evidence that personalities within breeding pairs and social groups can affect reproductive success and social group cohesion (Carlstead, Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999; Kuhar *et al*., 2006). Previous research has uncovered a link between personality and individual reproductive success in cheetahs (Wielebnowski, 1999), however the effects of personality on pair compatibility and social group cohesion have not been investigated in this species.

This research measures the behaviour, spatial association and personality of captive cheetahs housed in different social groups. It uses behavioural observations, Geographic

Information Systems (GIS) and keeper questionnaires to quantify captive cheetah social behaviour and personality. A new method of correcting indices of association to account for chance encounters allows the association patterns of group-housed cheetahs to be compared across institutions. The aim of the research is to determine the effects of social group housing and personality on the behaviour and reproductive success of captive cheetahs, and offer recommendations for improvements to current cheetah management practices.

1.2. Overview of the thesis

This thesis is organised into seven chapters. Chapter 1 outlined the background to the research and briefly stated the research aim. The second chapter presents a critical review of the literature on topics relevant to this research. It outlines issues relating to the maintenance of social groups in captivity and provides information on the current conservation status of wild cheetahs. The debate surrounding the cheetah's low genetic diversity, and its resulting conservation implications, is also explored. Previous studies of cheetah reproduction and behaviour, both in the wild and in captivity, are reviewed and a synthesis of the zoo animal personality literature is also presented. Chapter 2 concludes with a description of the aim, objectives and hypotheses of the research.

Chapter 3 provides an overview of the methods adopted for data collection. A number of methodological approaches were required to address the research objectives, including direct observations of cheetah behaviour, GIS to analyse a large spatial data set, and keeper questionnaires on cheetah personality. Each methodological approach is reviewed in Chapter 3 and a justification of its use in this research is presented.

Chapters 4, 5 and 6 are research chapters, which investigate the research objectives and, together, address the overall aim of the research. Each presents detailed procedures for the collection and analysis of the required data sets, the obtained results and a discussion of

the findings. The results of behavioural observations of cheetahs housed in natural and unnatural-type groups are presented in Chapter 4. Chapter 5 focuses on spatial association among group-housed cheetahs, and presents a new method for modelling chance encounters and correcting indices of association. Chapter 6 presents the results of the cheetah personality survey, and investigates the effect of personality on reproductive success and social group cohesion.

Finally, Chapter 7 presents a discussion of the findings of the research. It provides recommendations for further investigation and for improvements to current captive cheetah management practices.

2. Literature Review

2.1. Introduction

In this chapter, a critical review of the literature in the fields of cheetah conservation, biology, ecology and behaviour is presented. First, issues relating to the maintenance of social groups in captivity are outlined in Section 2.2, and the importance of the social environment in animal welfare and captive breeding is highlighted. A description of the current conservation status of wild cheetahs is provided in Section 2.3. Section 2.4 explores the debate surrounding the cheetah's low genetic diversity and the resulting conservation implications. Previous studies of captive cheetah reproduction and behaviour are reviewed in Section 2.5, and cheetah social organisation is described in Section 2.6. A review of the zoo animal personality literature is presented in Section 2.7 and the findings of previous studies of felid personality are reviewed in Section 2.8. Finally, Section 2.9 describes the aims and objectives of the research.

2.2. Maintenance of social groups in captivity

The success of captive breeding programmes is influenced by the well-being of individuals (Carlstead & Shepherdson, 1994; Ruiz-Miranda *et al*., 1998). Appropriate social group housing is an effective way of improving animal welfare by providing animals the context in which to express wild-counterpart behaviour (De Rouck *et al*., 2005; Price & Stoinski, 2007; Swaisgood & Schulte, 2010; Hosey *et al*., 2013). This can also affect reproductive success (Mellen, 1991; Carlstead & Shepherdson, 1994; Kleiman, 1994; Lindburg & Fitch-Snyder, 1994; Wielebnowski, 1998), educate zoo visitors about the behaviour of wild animals (Caro, 1993) and optimise the use of available accommodation.

The presence of conspecifics may function as a source of environmental enrichment for captive animals, providing opportunities for social interaction and adding an element of unpredictability to the captive environment (Carlstead, 1996; Young, 2003; Hosey *et al*., 2013). Indeed, social stimulation was found to be more effective than novel objects in reducing abnormal behaviours in laboratory-housed squirrel monkeys (*Samiri sciureus*: Spring *et al*., 1997). Group-housed monkeys displayed affiliative interactions and more active behaviours than singly-housed monkeys, and abnormal behaviours were more prevalent in singly-housed monkeys, regardless of the provision of novel objects (Spring *et al*., 1997). Similarly, Schapiro *et al*. (1996) found that group-housed rhesus monkeys (*Macaca mulatta*) spent less time engaged in abnormal behaviours than singly-housed individuals. There is also evidence that the presence of familiar conspecifics can ameliorate the physiological and behavioural effects of environmental stressors (Gust *et al*., 1994; Smith *et al*., 1998; Schaffner & Smith, 2005; Shutt *et al*., 2007; Aureli & Yates, 2010). Schaffner and Smith (2005) found that cortisol levels in an established pair of female captive Wied's marmosets (*Callithrix kuhlii*) were lower than in a newly formed pair following relocation. Aureli and Yates (2010) found that crested black macaques (*Macaca nigra*) displayed fewer self-directed behaviours, potential indicators of anxiety, following a bout of allogrooming. They suggested that allogrooming led to increased tolerance and the prevention of distress.

In contrast, inappropriate social groupings in captivity can have negative consequences for animal welfare, including chronic stress and social tension (Morgan & Tromborg, 2007; Price & Stoinski, 2007; Swaisgood & Schulte, 2010). Morgan and Tromborg (2007) reported that Japanese macaques (*Macaca fuscata*) maintained in all male groups, rather than the multi-male, multi-female groups observed in the wild, constantly monitored members of the group and displayed high levels of social tension. Davis *et al*. (2009) carried out a survey of aggressive interactions in 26 groups of spider monkeys (*Ateles*

spp.) housed at 24 zoos. The results revealed that male-male aggression was common, and that 23% of aggressive incidents resulted in lethal or fatal injury. This is in contrast with observations of aggression in wild social groups, which suggest that interactions among males are mostly affiliative (Davis *et al*., 2009). In wild populations, females disperse from their natal group and related males remain together. The authors suggested that the common practice of transferring males between zoos and housing unrelated males together may contribute to increased aggression and social tension, and recommended a change in management practices in order to create more natural social groups in captivity (Davis *et al*., 2009).

Some species can be successfully maintained in groups that have not been observed in wild populations. The availability of resources (especially food) in captivity allows for flexibility in the types and sizes of social groups that can be maintained. This, coupled with the constraints of finite enclosure space, has led to the housing of naturally solitary species in social groups (Price & Stoinski, 2007; Swaisgood & Schulte, 2010). Some animals benefit from this practice and adapt well to living in a group. Orang-utans (*Pongo pygmaeus* and *Pongo abelii*), for example, would not normally live in social groups in the wild but are often successfully group-housed in zoos (Perkins, 1992; Price & Stoinski, 2007). Perkins (1992) found a positive relationship between activity and group size in captive orang-utans, indicating the benefits of social interaction for this otherwise solitary species. Group-housed orang-utans engaged in more active behaviours than singly housed individuals, including allogrooming and social play. Similarly, Shepherdson *et al*. (2013) found that stereotypic pacing in polar bears (*Ursus maritimus*) decreased as group size increased, challenging the notion that captive polar bears should be maintained singly. However, not all solitary species can be successfully housed with conspecifics.

The majority of felid species are solitary and do not form social groups (MacDonald, Mosser *et al*., 2010). Previous research has indicated that captive felids can suffer chronic stress and reduced reproductive success when housed in groups (Mellen, 1991; Jurke *et al*., 1997; Mellen *et al*., 1998; Wielebnowski, Ziegler *et al*., 2002; Swanson *et al*., 2003). Mellen *et al*. (1998) observed more pacing behaviour, typically associated with poor welfare, in small felids housed in groups of three than those housed in pairs. Jurke *et al*. (1997) concluded that elevated faecal cortisol levels of socially housed female cheetahs indicated chronic physiological stress, which led to reproductive suppression in some individuals. Similarly, Wielebnowski and colleagues (Wielebnowski, Ziegler *et al*., 2002) found that female cheetahs housed in pairs displayed increased pacing behaviour and aggression, and reduced ovarian activity than did singly housed females. Even individuals that do not display outward behavioural signs of stress, and appear to be compatible, may not reproduce successfully (Kleiman, 1994). In contrast, some felid species thought to be solitary in the wild have been successfully housed in pairs or groups in captivity. Pair housed female tigers (*Panthera tigris* spp.) spent less time pacing than singly housed tigers (De Rouck *et al*., 2005). Similarly, Macri and Patterson-Kane (2011) observed less pacing in pair housed than singly housed snow leopards (*Uncia uncia*), and affiliative interactions between pair housed animals. It may be the case that these species are not strictly solitary in the wild, as first thought.

Housing animals in social groups resembling those that have been observed in wild populations can have a direct effect on reproductive success (Mellen, 1991; Carlstead & Shepherdson, 1994; Kleiman, 1994; Lindburg & Fitch-Snyder, 1994; Wielebnowski, 1998; Swaisgood & Schulte, 2010). In her study of 20 small felid species (genus: *Felis*), Mellen (1991) found a negative correlation between group size and reproductive success. The species in Mellen's study, including margays (*Felis wiedii*), ocelots (*Felis pardalis*) and servals (*Felis serval*), are solitary in the wild, with males and females only coming into contact for mating

(Mellen, 1991). This was reflected in the results, since captive felids housed in groups larger than male-female pairs were unlikely to successfully reproduce (Mellen, 1991).

Inappropriately small groups can also have negative consequences for reproductive success. Bardi *et al*. (2001) found an effect of social group size on parental success in cotton-top tamarins (*Saguinus oedipus*). Infants were more likely to be successfully reared in the presence of helpers to assist with parental care. In their retrospective study of mortality in the same species, Leong *et al*. (2004) found that litters of triplets had lower survivorship than twins. The authors suggested that this resulted from the parents' inability to care for three offspring, and postulated that survival may be higher for triplets if they are born into a social group containing older siblings. Similar correlations between infant survival and the number of available helpers have also been found in wild tamarins (Price, 1992). This has implications for the housing of captive groups, as infant mortality in this species is likely to be high if group size is too small (Price & Stoinski, 2007).

Research by Carlstead and her colleagues (Carlstead, Fraser *et al*., 1999; Carlstead & Brown, 2005) revealed the effects of the social environment on reproduction in black rhinoceros. A survey of black rhino behaviour, housing and reproductive success found that zoos housing only one female had better institutional breeding success than zoos housing groups of two or more females (Carlstead, Fraser *et al*., 1999). Furthermore, the forced proximity of conspecifics was also associated with a physiological stress response (Carlstead & Brown, 2005). Given that field observations indicate that black rhinos in the wild are asocial, this led to the recommendation that zoos maintain male-female pairs and keep them separated, except for breeding introductions (Carlstead, Fraser *et al*., 1999; Carlstead & Brown, 2005; Swaisgood & Schulte, 2010). In contrast, wild white rhinoceros (*Ceratotherium simum*) females have been observed in social groups, and zoos housing females in groups of two or more had better reproductive success than those housing females singly (Swaisgood *et*

al., 2006). Taken together, these results highlight the importance of using information from the field to inform appropriate groupings in captivity to facilitate reproductive success.

The social environment can have a profound effect on the behaviour, welfare and reproductive success of captive animals and care should be taken to provide animals with appropriate social stimulation (Morgan & Tromborg, 2007; Price & Stoinski, 2007; Hosey *et al*., 2013). This requires knowledge of the social systems and behaviour of animals in their natural habitat, as well as careful monitoring of the behaviour of social groups in captivity (Price & Stoinski, 2007; Swaisgood & Schulte, 2010). Appropriate social group housing can improve animal welfare and reproductive success, which in turn affects the success of captive breeding programmes (Carlstead & Shepherdson, 1994; Kleiman, 1994; Lindburg & Fitch-Snyder, 1994).

2.3. Current status of the cheetah in the wild

Despite the large range in body size and habitat preferences of felid species, their morphology and behaviour is remarkably similar, perhaps because they are all strict carnivores with a preference for vertebrate prey (Macdonald, Loveridge *et al*., 2010). Habitat and predatory specialisations may leave felids vulnerable to climate change and anthropogenic conflict (Karanth & Chellam, 2009; Macdonald, Loveridge *et al*., 2010); felids occur at low population densities, have large home ranges and their feeding habits often place them in competition with humans (Inskip & Zimmerman, 2008; Karanth & Chellam, 2009). Of the 36 extant species of felids, 16 are included in the top three threat categories (Critically Endangered, Endangered and Vulnerable) on the IUCN Red List (Macdonald, Loveridge *et al*., 2010), including the cheetah (Durant *et al*., 2008; Macdonald, Loveridge *et al*., 2010).

Based on molecular evidence, the phylogeny of the Felidae can be subdivided into eight clades (Johnson & O'Brien, 1997; Johnson *et al*., 2006; Werdelin *et al*., 2010).

Although the morphological features of the cheetah once caused it to be placed in a monophyletic group (Caro, 1994; Russell & Bryant, 2001), recent phylogenetic analyses place the cheetah within the *Puma* lineage (Johnson *et al*., 2006; O'Brien *et al*., 2008; Werdelin *et al*., 2010), alongside the puma (*Puma concolor*) and the jaguarundi (*Puma yagouaroundi*). The cheetah is the only extant species of the genus *Acinonyx* (O'Brien *et al*., 1985, 2008; Werdelin *et al*., 2010), of which there are five recognised sub-species: *Acinonyx jubatus hecki*; *A. j. jubatus*; *A. j. raineyi*; *A. j. soemmeringii* and *A. j. venaticus* (Caro, 1994; Krausman & Morales, 2005).

Latest estimates suggest that the wild cheetah population numbers between 7,000 and 10,000 individuals (Durant *et al*., 2008). Cheetah population estimates have proved difficult, since cheetahs are poor users of National Parks and range over wide areas of unprotected land (Gros, 2002; Marker, Dickman *et al*., 2003; Durant *et al*., 2008). However, it is thought that numbers of cheetahs in areas that have not been extensively surveyed are unlikely to raise the population estimate above 10,000 individuals (Durant *et al*., 2008). The effective population size (the estimated percentage of the population that is actively reproducing and passing on its genes to the next generation) could be less than half of the actual adult population (Kelly, 2001; Durant *et al*., 2008). Kelly's (2001) analysis of the Serengeti cheetah population revealed an effective population size of 44%, with only a few females raising offspring to maturity and contributing to the next generation, and leaving the population at risk of genetic loss and inbreeding. However, evidence for female promiscuity and litters of cubs with mixed paternity (Gottelli *et al*., 2007) casts doubt on the findings of Kelly (2001) and indicates that male cheetahs pass on genes more effectively than expected. Thus, rates of genetic loss may well be lower than implied by Kelly's (2001) findings.

Threats to the remaining cheetah population include habitat loss and fragmentation (Merola, 1994; Marker-Kraus & Kraus, 1997; Gros, 2002; Durant *et al*., 2008), declining prey

numbers (Gros, 2002) and predation by lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) (Laurenson, 1994; Durant, 1998; Marker, Dickman *et al*., 2008). In Namibia, cheetahs are increasingly coming into conflict with farmers, who blame cheetahs for livestock losses, and are often shot on sight (Marker-Kraus & Kraus, 1997; Marker, Dickman *et al*., 2003; Marker, Kraus *et al*., 2003; Inskip & Zimmerman, 2008; Durant *et al*., 2010). There is also some debate over the genetic health of the cheetah, with the discovery that the species exhibits extremely low levels of heterozygosity (O'Brien *et al*., 1983, 1985).

2.4. Low genetic variation in the cheetah

The cheetah is well known to conservation biologists as an example of a species that is vulnerable to extinction due to a lack of genetic variation (Caro, 2000). Following two influential papers (O'Brien *et al*., 1983, 1985), a lack of genetic variability was proposed as an explanation for the low population density of cheetahs in the wild (Caro, 2000; Kelly & Durant, 2000). Low levels of heterozygosity can have a negative impact on survival and reproductive success (O'Brien *et al*., 1983; Allendorf & Leary, 1986; Ralls *et al*., 1988; Brown *et al*., 1996; Crnokrak & Roff, 1999; Slate *et al*., 2000) and might leave a population vulnerable to disease (O'Brien *et al*., 1985; Allendorf & Leary, 1986) and juvenile mortality (O'Brien *et al*., 1985; Ralls *et al*., 1988; Yuhki & O'Brien, 1990; Wielebnowski, 1996; Crnokrak & Roff, 1999; Caro, 2000), both of which are signs of inbreeding depression (O'Brien *et al*., 1985; Ralls *et al*., 1988; Yuhki & O'Brien, 1990; Merola, 1994; Crnokrak & Roff, 1999).

O'Brien *et al*. (1983) examined fibroblasts from 50 cheetahs using two-dimensional gel electrophoresis. They found that the entire sample was monomorphic at 47 loci, and average heterozygosity (0.013) was particularly low, compared to other mammalian species. The authors suggested a population bottleneck, followed by inbreeding, as a possible

explanation for their findings. In a further study, O'Brien *et al*. (1985) found that unrelated cheetahs accepted reciprocal skin grafts, indicating extremely low levels of variation at the Major Histocompatibility Complex (MHC), a group of loci that are usually highly polymorphic (O'Brien *et al*., 1985; Yuhki & O'Brien, 1990; Caro, 2000). They also presented evidence of high juvenile mortality in captivity, and described a case of feline infectious peritonitis, which spread through a captive population in Oregon, causing the deaths of 18 out of 42 individuals whilst leaving other felid species unaffected. O'Brien *et al*. (1985) argued that these results supported the hypothesis that the cheetah's lack of genetic variation had left it vulnerable to extinction.

In light of this evidence, it would seem that little can be done to conserve a species that exhibits such low genetic variation as the cheetah. However the importance of the cheetah's lack of genetic variation may have been overstated, as possible alternative explanations for low population density in the wild have emerged in the literature. Research into the behaviour and ecology of wild cheetahs has provided evidence that, despite a lack of genetic variation, cheetahs are able to survive and successfully reproduce (Laurenson *et al*., 1992; Laurenson, 1994; Caro, 2000; Kelly & Durant, 2000; Gottelli *et al*., 2007). In particular, field studies in the Serengeti carried out by Laurenson and her colleagues (Laurenson *et al*., 1992; Laurenson, 1993, 1994) provided evidence for the ecological problems faced by cheetahs in the wild. Juvenile mortality in the Serengeti population is extremely high, with estimates of up to 98% of cubs dying before independence (Laurenson *et al*., 1992). This might be a symptom of inbreeding depression (Merola, 1994), caused by a lack of genetic variation (O'Brien *et al*., 1985). However, field observations contradict this hypothesis. Laurenson (1994) observed 36 litters of cubs born to 17 mothers during a three-year period. Of 119 cub deaths, 73% were estimated to have been caused by predation, 78% of these by lions. Other causes of death included environmental incidents (e.g. fire, 14.4%)

and abandonment or starvation (8.2%). Only 4.2% of deaths were estimated to be the result of inviable cubs. Thus, Laurenson and her colleagues argued that there is little evidence for mortality resulting from low genetic variation. Rather, ecological factors, particularly predation by lions, are the likely causes of cheetah cub mortality (Laurenson *et al*., 1992; Laurenson, 1994).

Further evidence against the genetic variation hypothesis comes from field studies in Namibia and Botswana. Lions and hyenas are largely absent from Namibian farmland (Marker, Dickman *et al*., 2003, 2008), so intra-guild competition is lower than in the Serengeti. Marker, Dickman *et al*. (2003) followed 412 cheetahs on Namibian farmland between 1991 and 2000, and examined social structure, reproductive parameters, mortality and survivorship. They found that 75% of cubs survived the first twelve months after emerging from the lair, a 25% mortality rate. Unlike Laurenson's (1994) study, Marker and her colleagues (Marker, Dickman *et al*., 2003) were unable to ascertain mortality rates prior to emergence from the lair. Nevertheless, in the absence of natural predators, juvenile mortality was much lower than in the Serengeti, where cheetahs are in competition with lions and hyenas (Marker, Dickman *et al*., 2003). In a further study, Mills and Mills (2014) found that overall cheetah cub survival was significantly higher in the Kgalagadi (Kalahari) Transfrontier Park (KTP), Botswana, than in the Serengeti. They stated that at least one cub survived to adolescence in 45% of KTP litters, compared with only 9.7% of Serengeti litters. This was despite the presence of predators such as lions, hyenas and leopards (*Panthera pardus*). These findings provide further evidence that juvenile mortality is not simply a result of low heterozygosity, and the observed variation in juvenile mortality rates in different areas casts further doubt on the influence of low genetic variation on cheetah population density.

The captive cheetah population was used by O'Brien *et al*. (1985) to provide more evidence of the consequences of low genetic variation. They argued that the problems of poor

reproductive success, disease susceptibility and high juvenile mortality observed in captive cheetahs were a result of a lack of genetic variation. Wielebnowski (1996) investigated captive juvenile mortality rates, using zoo records and the International Cheetah Studbook. She found that inbred cubs, whose parents were related, were more likely to die before independence than non-inbred cubs. Wielebnowski (1996) argued that if low genetic variation was the sole cause of infant mortality, non-inbred cubs would be expected to be just as susceptible to early death as inbred cubs. Moreover, this study uncovered variation in juvenile mortality rates among zoos, which would also not be expected if a lack of genetic variation was the sole cause, and may be explained by variation in management and husbandry practices.

It now seems that the cheetah's lack of genetic variation at the species level is not the only factor contributing to the low population density of wild cheetahs. Recent research has revealed that the problems faced by cheetahs are ecological, rather than genetic (Caro & Laurenson, 1994; Caro, 2000; Castro-Prieto *et al*., 2011; Mills & Mills, 2014). These problems represent a more immediate threat to the cheetah population than inbreeding depression, as their effects will be felt more quickly (Caro & Laurenson, 1994). Conservation strategies such as land use planning (Durant *et al*., 2008; Marker, Dickman *et al*., 2008), restoration of suitable cheetah habitat (Marker, Dickman *et al*., 2008) and reducing human-cheetah conflict (Marker-Kraus & Kraus, 1997; Marker, Dickman *et al*., 2008) can contribute to improving the outlook for the cheetah in the wild. Following the successful reintroductions of captive cheetahs to protected areas by the Cheetah Conservation Fund in Namibia (Marker, 2012b), and to Sir Yani Bas Island in Dubai (McKeown, 2010), there is the potential for more captive individuals to be released in the future. Thus, a carefully managed captive breeding programme has the capability to contribute to cheetah conservation in the long term.

2.5. Cheetah reproduction in captivity

The rapid decline in the wild cheetah population has led to the development of co-ordinated captive breeding programmes, in order to try and increase cheetah numbers (Caro, 1993; Marker-Kraus & Kraus, 1997; Bauman *et al*., 2010). The European Endangered Species Programme (EEP) and the Species Survival Plan (SSP) are carefully managed to prevent inbreeding. The International Cheetah Studbook contains information about the captive cheetah population dating from 1969 (Marker, 2012c), and recommendations for breeding pairs are made by the studbook keeper on the basis of kinship. Unfortunately, many collections have encountered problems with breeding cheetahs. Low conception rates, irregular oestrus cycles and periods of anoestrus in females, and the failure of recommended pairs to reproduce (Caro, 1993; Brown *et al*., 1996; Asa *et al*., 2011; Wachter *et al*., 2011) have resulted in a captive population that is not self-sustaining (Wildt *et al*., 1993; Wielebnowski, Ziegler *et al*., 2002; Crosier *et al*., 2007; Bauman *et al*., 2010; Marker, 2012c). During 2011 only 90 animals (44 males and 46 females), representing 5.6% of the captive cheetah population, bred successfully and of 241 facilities that maintained cheetahs, only 33 (13.7%) had reproductive success (Marker, 2012c). This is of concern because poor reproductive success can indicate captive welfare problems, and is particularly puzzling, given that wild cheetahs appear to show no evidence of reproductive difficulties (Laurenson *et al*., 1992; Lindburg *et al*., 1993; Laurenson, 1994; Merola, 1994; Brown *et al*., 1996; Kelly *et al*., 1998; Caro, 2000; Wielebnowski, Ziegler *et al*., 2002; Gottelli *et al*, 2007).

Wild and captive cheetahs share their lack of genetic diversity (O'Brien *et al*., 1985; Caro, 1993; Lindburg *et al*., 1993; Brown *et al*., 1996), however wild cheetahs show a high rate of reproduction. An estimated 80% of adults in the wild produce offspring (Laurenson *et al*., 1992), compared to only 5.6% of captive individuals in 2011 (Marker, 2012c). In a study of wild female cheetahs in the Serengeti, Laurenson *et al*. (1992) reported that only two of 14

radio-collared adult females failed to reproduce during a three-year study period, and only one young female in the study had never had cubs. Furthermore, females were capable of conception even before their previous litter had left and, where a female's previous litter died, the next successful conception occurred within three weeks (in some cases, as soon as two days) after the loss of the litter (Laurenson *et al*., 1992). These findings confirm that cheetahs in the wild are behaviourally and physiologically capable of reproduction, and the authors proposed that it is high rates of juvenile mortality, rather than an inability to conceive, that limits wild cheetah numbers. It would seem, therefore, that an inability to conceive in captivity is a result of some aspect of the captive environment (Laurenson *et al*., 1992).

In addition to genetic diversity, reproductive physiology has also been investigated in captive cheetahs. A survey by Wildt *et al*. (1993) of 128 cheetahs in 18 zoos revealed that males consistently produced structurally abnormal sperm, and more than 50% of females had inactive ovaries. The authors also found no differences in reproductive anatomy and physiology between proven breeders and those individuals that had never bred. Sperm abnormalities in cheetah ejaculates had previously been reported (Wildt *et al*., 1983, 1987), with further investigations revealing no differences in the proportion of structurally abnormal sperm found in ejaculates of wild and captive individuals (Wildt *et al*., 1987). It is likely that these observed sperm abnormalities are linked to the cheetah's low genetic diversity (Wildt *et al*., 1983, 1987). Despite this, copulation still leads to fertilisation (Lindburg *et al*., 1993; Wielebnowski & Brown, 1998), and females can become pregnant after only one mating (Caro, 2000).

Brown *et al*. (1996) analysed the reproductive activity of 26 female cheetahs at five zoos, using faecal steroids. They found that 75% of the cheetahs exhibited evidence of oestrous cyclicity, although all individuals exhibited periods of anoestrus between two and five months in duration, which did not appear to be seasonal. Social groupings varied between

zoos and females were housed together "at least occasionally" (Brown *et al*. 1996, p. 338).

Wielebnowski and Brown (1998) attempted to correlate behavioural observations with ovarian activity. They found that several behaviours thought to be indicative of oestrus were positively correlated with faecal oestradiol concentrations. They also found no differences in average oestradiol concentrations between females that had bred successfully and females that, despite being introduced to males on several occasions, had not ever bred. The social groupings of the females in this study also varied, with some females housed together constantly, some housed together occasionally and others housed alone. The authors also noted that males and females, whilst housed separately, were frequently kept in adjacent enclosures. However, social factors were not included in the discussion of the results of this study.

The captive environment does not appear to impair physiological function in cheetahs (Wildt *et al*., 1987; Wielebnowski & Brown, 1998; Crosier *et al*., 2007) and wild and captive cheetahs share the same lack of genetic diversity (O'Brien *et al*., 1985; Caro, 1993; Lindburg *et al*., 1993; Brown *et al*., 1996). It is likely, therefore, that the reasons for the cheetah's poor reproductive performance in captivity are related to the behaviour and management of the species (Laurenson *et al*., 1992; Caro, 1993; Lindburg *et al*., 1993; Wielebnowski, 1996; Wielebnowski & Brown, 1998; Wielebnowski, Ziegler *et al*., 2002; Crosier *et al*., 2007; Bauman *et al*., 2010). Knowledge of cheetah behaviour is crucial if the captive breeding programme is to be successful (Laurenson *et al*., 1992; Lindburg & Fitch-Snyder, 1994), yet the research emphasis in the captive setting has so far been placed on genetics and reproductive physiology. An important aspect of captive cheetah management that has thus far received little attention is social group housing (Caro & Collins, 1986; Caro, 1993; Wielebnowski, Ziegler *et al*., 2002; Bauman *et al*., 2010).

2.6. Cheetah social organisation

The influence of the social environment on the welfare and breeding success of captive wild animals was outlined in Section 2.2 of this chapter. The cheetah's social organisation is rare among mammals, and its complexity has been revealed by extensive field observations (Eaton, 1970; Schaller, 1972; Caro & Collins, 1986; Caro, 1994; Marker, Dickman *et al*., 2003; Durant *et al*., 2004; Gottelli *et al*., 2007). However, little is currently known about the effects of social group housing on captive cheetah behaviour (Ruiz-Miranda *et al*., 1998; Bauman *et al*., 2010).

2.6.1. Sociality in wild cheetahs

In the wild, adult females are solitary unless accompanied by cubs (Caro, 1994; Wielebnowski, Ziegler *et al*., 2002; Terio *et al*., 2003). During an extensive study of wild cheetahs in the Serengeti, Caro (1994) reported that cubs separated from their mothers at approximately 18 months of age, remaining in sibling groups for an average of 6.7 months with females separating from their littermates between the ages of 23 and 27 months. Females do not hold territories, but have large, undefended home ranges which vary in size depending on environmental conditions (Caro, 1994; Durant *et al*., 1988, 2008; Marker, Pearks Wilkerson *et al*., 2008). The average home range size of a female in the Serengeti is around 800km^2 (Caro, 1994; Gottelli *et al*., 2007). Here, prey is migratory and females travel long distances to follow herds of Thomson's gazelles (*Gazella thomsoni*), which constitute up to 90% of their diet (Schaller, 1972; Durant *et al*., 1988, 2010; Caro, 1994). In Namibia, female home range size can be as large as 1,836km^2 (Marker, Dickman *et al*., 2008). Reasons for the marked difference in the home range sizes of Namibian and Serengeti cheetahs are unclear, but Marker and her colleagues (Marker, Dickman *et al*., 2008) speculated that lower rainfall in Namibia might lead to reduced prey density, causing cheetahs to range further.

Nonetheless, in both Namibia and the Serengeti, the home ranges of females show considerable overlap and it is common for a number of females to use the same area (Caro, 1994; Durant, 1998; Durant *et al*., 2010). However, whilst there are conflicting reports of female cheetahs tolerating one another and congregating around resources (Durant, 1998; Durant *et al*., 2010) as well as actively avoiding one another (Caro, 1994), there is no evidence of wild adult females living together in social groups (Schaller, 1972; Caro, 1994).

Whilst female cheetahs are solitary and not territorial, males can live alone or in small groups and either hold territories or range over large areas. Caro (1994) categorised males as either "resident" or "non-resident". Resident males were "repeatedly seen in the same small area over a period of months, and urine marked the area" (Caro 1994, p. 203). Non-resident males "were seen in several different areas, often many kilometres apart" (Caro 1994, p. 204) and were not observed scent marking. Thus, resident males were those that maintained and defended a territory, whilst non-resident males were unable to acquire a territory, or had been displaced from a previously held territory (Caro, 1994). Non-resident males range over large areas of around 800km^2 (Durant *et al*., 1988; Caro, 1994; Gottelli *et al*., 2007) and are more likely to exhibit signs of stress, such as raised cortisol levels, and poor physical condition, including mange and hair loss, than residents (Caro *et al*., 1989; Caro, 1994). They also spend more time alert and sitting up, monitoring their surroundings, than resident males, and less time resting in exposed locations (Caro *et al*., 1989; Caro, 1994).

Up to 60% of males remain in stable groups, or coalitions, throughout their lifetime (Caro & Collins, 1986; Caro, 1993, 1994; Ruiz-Miranda *et al*., 1998; Marker, Dickman *et al*., 2003; Durant *et al*., 2004). Coalitions are better able to occupy territories than single males (Caro & Collins, 1986; Durant *et al*., 2004), and males holding territories are in better physical condition than non-resident males (Caro *et al*., 1989). In the Serengeti, coalitions of males hold territories of around 40km^2 within female home ranges, and their territories

contain resources, such as water and vegetation cover, that are attractive to females (Caro & Collins, 1987). Coalitions almost always consist of brothers (Caro, 1994; Marker, Pearks Wilkerson *et al*., 2008). Caro and Durant (1991) used differences in coat patterns, particularly widths of tail bands, to show that males living in coalitions were related. Using a quantitative scoring system, they found that the tails of littermates resembled one another more closely than the tails of unrelated individuals.

Further field studies suggest that unrelated males may also join up with littermates to form coalitions of three or four individuals (Caro, 1993, 1994). Where there is intense competition for suitable territory sites, it is advantageous for unrelated males to form groups, as well as related males (Caro, 1994; Durant *et al*., 2010). Caro (1994) reported that coalitions of two individuals were likely to consist only of littermates and coalitions of three individuals were likely to be composed of two littermates and one non-relative. The formation of coalitions containing an unrelated male is thought to occur before three years of age (Caro, 1993).

Coalition members maintain close proximity to one another and intra-group interactions are mostly affiliative, with frequent displays of allogrooming (Caro, 1993, 1994). In Caro's (1994) study, grooming was initiated equally in some coalitions, and unequally in others. Grooming was reciprocated on more than 50% of occasions and the initiation of grooming between littermates was equal, however siblings preferred to groom one another rather than a non-relative. Overt aggression between coalition members is rare, even around kills and during encounters with females (Caro, 1993, 1994). This is probably because the risks of injury to themselves or their coalition-mates are greater than the short-term benefits resulting from conflicts (Caro, 1994). Coalitions are egalitarian associations and there appears to be no dominance hierarchy within cheetah groups (Caro, 1994). Activities such as grooming and hunting often are initiated equally by different members of the group, and

group members spend equal time feeding from carcasses (Caro, 1994). Caro (1994) suggested that the similar body size of males means that monopolisation of food or females by one group member is difficult, and that any kind of dominance hierarchy is unlikely.

Group living is unusual in felid species (Kitchener, 2000; Macdonald, Mosser *et al*., 2010) but the formation of male coalitions has been described in other mammals (e.g. banded mongooses (*Mungos mungo*): Waser *et al*., 1994; chimpanzees (*Pan troglodytes*): Mitani *et al*., 2000; red fronted lemurs (*Eulemur fulvus rufus*): Ostner & Kappeler, 2004; fossas (*Cryptoprocta ferox*): Lührs *et al*., 2013). Coalitions can be characterised by mutual tolerance and collaboration (Olson & Blumstein, 2009), and possible benefits of coalition formation include increased foraging success (Blundell *et al*., 2002; Lührs *et al*., 2013), protection from predators (Waterman, 1997), increased access to reproductive females (Packer & Pusey, 1982; Lührs *et al*., 2013) and support by group members in conflicts or aggressive interactions (Waser *et al*., 1994; Ostner & Kappeler, 2004).

Increased hunting or foraging success has been observed in coalitions of river otters (*Lontra canadensis*: Blundell *et al*., 2002) and fossas (Lührs *et al*., 2013). Thus, one possible explanation for group living in cheetahs might be co-operative hunting, as also evident in lions, the only other felid species known to form stable social groups (Schaller, 1972; Caro, 1994; Kitchener, 2000; Macdonald, Mosser *et al*., 2010). Although larger groups of cheetahs hunt larger prey than Thomson's gazelles (e.g. wildebeests, *Connochaetes taurinus*), hunts by groups of cheetahs are no more successful than hunts by single cheetahs (Caro, 1994). Furthermore, cheetah hunts are rarely co-ordinated and not all group members always contribute to a hunt (Caro, 1994). Thus, rather than co-operative hunting, it is likely that group living in cheetahs is better explained by intra-specific competition, as male reproductive success is limited by access to females (Caro, 1994; Durant *et al*., 2004; Gottelli *et al*., 2007).

Reproductive coalition formation occurs when males collaborate to increase the potential for group members to gain access to females (Olson & Blumstein, 2009). This may be through the defence or monopolisation of females (Lührs *et al*., 2013), ousting resident males from an existing social group (Waser *et al*., 1994) or the defence of a territory within a female's home range (Wagner *et al*., 2008). Lührs *et al*. (2013) found that male fossas living in pairs were better able to successfully mate with females during the breeding season than solitary males. This may have been because their increased body mass, resulting from co-operative hunting, allowed them to monopolise females more easily (Lührs *et al*., 2013). In striped hyenas (*Hyaena hyaena*), groups of males defend territories within the home ranges of solitary females, against other males (Wagner *et al*., 2008). Whilst this may seem counter-intuitive, Wagner *et al*. (2008) suggested that it was advantageous for a male to co-operatively defend a territory and share access to a female, rather than to attempt, and fail, to defend a female alone.

Cheetah coalition territories have been shown to overlap female home ranges (Caro, 1994; Broomhall *et al*., 2003). Thus, females are often observed within territories held by coalitions and coalition members attempt to mate with females passing through (Caro, 1994; Durant *et al*., 2004; Gottelli *et al*., 2007). There is evidence that litters of cubs can be of mixed paternity, indicating that females mate with multiple males in the same reproductive cycle (Gottelli *et al*., 2007). Consequently, remaining in a coalition may benefit males by affording them increased access to females, and better opportunities to monopolise females in oestrus (Caro, 1994; Gottelli *et al*., 2007). The low levels of aggression within coalitions in the presence of females might indicate that coalition members gain equal access to females in the long term (Caro, 1994). Given that there is no evidence for a dominance hierarchy among males, it is not the case that one member of the coalition is dominant and the others are non-reproductive helpers. However, littermates do gain reproductive benefits by aiding their

siblings (Caro, 1994; Durant *et al*., 2004; Gottelli *et al*., 2007). An individual's lifetime reproductive success can therefore be increased by remaining in a coalition, even though access to females must be shared (Wagner *et al*., 2008; Olson & Blumstein, 2009).

2.6.2. Cheetah social groups in captivity

The Association of Zoos and Aquariums (AZA) Husbandry Manual for the cheetah states that males can be housed either singly or in coalitions, and that male siblings should remain together for life (Ziegler-Meeks, 2009). In light of their solitary nature in the wild, females recommended for breeding should be housed separately, but the husbandry manual also states that individuals not recommended for breeding can be housed in compatible single-sex or mixed-sex groups (Ziegler-Meeks, 2009). Consequently, there is variation in current housing practices and captive cheetahs are maintained singly, in pairs and in groups of three or more. Indeed, the females studied by Brown *et al*. (1996) and Wielebnowski and Brown (1998) were maintained in highly variable social groups. Some females were housed alone, some were constantly group-housed and some were occasionally group-housed.

Despite the recommendations in the husbandry manual, there has been little effort to systematically document the behaviour of cheetahs housed in different social groups. Jurke *et al*. (1997) investigated the relationship between cortisol excretion and ovarian activity in seven captive females at the San Diego Wildlife Park (California, USA). They observed increased cortisol excretion by females exhibiting decreased ovarian activity, and suggested that the presence of conspecifics is a source of chronic stress. However, they were unable to investigate the effects of changes in social groupings due to space restrictions.

In a later study, Wielebnowski and her colleagues (Wielebnowski, Ziegler *et al*., 2002) investigated the effects of changing social conditions on the behaviour, ovarian activity and adrenal activity of female cheetahs. Females were housed in pairs for six months, and then

maintained individually. Agonistic behaviour was observed in five of six pairs and affiliative behaviour was observed in one pair, consisting of a mother and daughter. Pair-housed females also showed increased pacing behaviour, and ten of twelve individuals only paced when they were pair-housed. No changes in adrenal activity were detected, but analyses of faecal oestradiol and progestogen concentrations revealed that pair-housed females exhibited long periods of anoestrus, which, interestingly, did not occur when the pairs were separated. The authors concluded that, given their observations of pacing behaviour and reproductive suppression, housing females in groups should be avoided.

Whilst the effects of social group housing on female behaviour have been investigated to an extent, even fewer published studies have focused on the behaviour of captive males. It seems that the formation and maintenance of coalitions is important for improving the survival and reproductive success of wild male cheetahs (Ruiz-Miranda *et al*., 1998; Durant *et al*., 2004; Gottelli *et al*., 2007). Given the importance of sociality in the wild, housing male cheetahs in coalitions in captivity may therefore have implications for welfare and reproductive success (Caro, 1993; Ruiz-Miranda *et al*., 1998).

Ruiz-Miranda *et al*. (1998) studied the behaviour of two coalitions of captive male cheetahs during separation and reunion trials. They observed increases in vocalisation and pacing when coalition members were separated from one another, and increased affiliative behaviours when they were reunited. Interestingly, the intensity of these behaviours was more pronounced in siblings than non-siblings and the authors concluded that their findings indicated a degree of psychological attachment between coalition members (Ruiz-Miranda *et al*., 1998). In a similarly conducted study on the behaviour of four male cheetahs housed together in the same enclosure (Chadwick *et al*., 2013), I observed a closer association within a sibling pair and a half sibling pair, than between the pairs. Furthermore, following the relocation of one of the cheetahs, the remaining males appeared to form a coalition of three,

as indices of association between the unrelated male and the siblings increased (Chadwick *et al*., 2013). However, few other published studies have focused on the social behaviour of males in captivity. Given the complex social system evident in wild cheetahs, there is a need for the social behaviour of captive individuals to be investigated further, especially in light of the difficulties encountered by zoos in breeding the species.

2.7. Animal personality

The success of captive breeding programmes depends not only on the management of the captive population as a whole, but also on the management and husbandry of individual animals. The captive environment itself has a profound effect on the behaviour of wild animals (Carlstead, 1996; Hosey, 2005; Morgan & Tromborg, 2007) and individuals vary in their responses to environmental variables (Carlstead, Mellen *et al*., 1999; Jones & Gosling, 2005; Kuhar *et al*., 2006; Hill & Broom, 2009). During the last fifteen years, there has been an emerging field of research concerned with the study of animal personality and its implications for the breeding, management and welfare of captive animals (Powell & Svoke, 2008).

There is inconsistency in the literature regarding the terms used when describing animal personality (Réale *et al*., 2007; Freeman & Gosling, 2010; Coleman, 2012). Many researchers refer to *temperament* (Freeman *et al*., 2004), others use the phrase *behavioural profiling* (Carlstead, Fraser *et al*., 1999; Carlstead *et al*., 2000) and still others refer to *individual differences* (Wielebnowski, 1999; Blumstein *et al*., 2006) or *individual distinctiveness* (Carlstead, Mellen *et al*., 1999). These differing terms are sometimes used interchangeably in the same paper (e.g. Blumstein *et al*., 2006).

Historically, distinctions were made in the psychology literature between the terms *temperament* and *personality* on the basis of age, with *temperament* describing behavioural

differences in children and *personality* describing differences in adults (Coleman, 2012; Watters & Powell, 2012). Further distinctions between the terms were made on a genetic basis, with some authors arguing that *temperament* had a genetic element, whilst *personality* did not (Coleman, 2012). Additionally, the term *personality* is considered by some authors to be too anthropomorphic to be used in the animal behaviour literature (Gosling, 2008; Weinstein *et al*., 2008; Meagher, 2009; Freeman & Gosling, 2010). However, little distinction is now made between the terms *temperament* and *personality* (Coleman, 2012), and there is little evidence to support the view that the results of animal personality research are distorted by anthropomorphism (Kwan *et al*., 2008; Weiss *et al*., 2012). Thus, despite previous disagreements in the literature, use of the term *personality* now seems to be more generally accepted (Gosling, 2008; Freeman & Gosling, 2010). The term *personality* is used hereafter, defined as "individual differences in behaviour that are thought to be stable across time and situations" (Freeman & Gosling 2010, p. 654).

There is a growing body of evidence that personality traits are heritable and affect fitness, and thus have evolutionary consequences (Weiss *et al*., 2000; Drent *et al*., 2003; Réale & Festa-Bianchet, 2003; Dingemanse *et al*., 2004; Dingemanse & Réale, 2005; McDougall *et al*., 2006; Réale *et al*., 2007; Smith & Blumstein, 2008). Natural selection may operate on personality traits (Réale & Festa-Bianchet, 2003; Dingemanse & Réale, 2005), and it has been suggested that variation in the personalities of individuals, leading to a variety of behavioural strategies to cope with challenging stimuli, results in a viable population (Dingemanse & Réale, 2005; Réale *et al*., 2007).

Dingemanse *et al*. (2004) demonstrated the fitness consequences of personality in great tits (*Parus major*). Individuals differed in their expression of exploratory behaviour in novel environments; fast explorers were bold and aggressive, whereas slow explorers were shy and non-aggressive. This trait was related to survival between breeding seasons and

offspring recruitment; however selection pressures changed during the three-year study. Resource abundance resulted in relaxed competition for food but increased competition for territories. The authors suggested that during resource-abundant years fast-exploring males benefited because they were better able to defend a territory, whilst slow-exploring females survived better because aggressive behaviour resulted in increased mortality. During years when resources were scarce, the opposite was true. Thus, selection favoured different personality types and maintained genetic variation in personality traits within the population (Dingemanse *et al*., 2004).

In their meta-analysis of the fitness consequences of personality, Smith and Blumstein (2008) found 31 publications correlating personality with reproductive success or survival. The results of their analysis indicated that, in general, bold individuals had better reproductive success than shy individuals, and that shy individuals exhibited greater longevity than bold individuals. This may be because bold individuals are more likely to approach novel stimuli and less likely to avoid potentially dangerous situations (Bremner-Harrison *et al*., 2004). Conversely, Réale and Festa-Bianchet (2003) found that bold bighorn sheep (*Ovis canadensis*) ewes were more likely to survive during periods of increased predation than shy individuals. One possible explanation for this is that bold individuals were more likely to inspect and deter predators than shy individuals, however no attacks by predators were observed by the authors and this prediction could not be tested (Réale & Festa-Bianchet, 2003).

There is great potential for personality assessments to be incorporated into zoo management practice to improve the welfare and breeding success of zoo mammals. The effect of individual differences on zoo animal behaviour and reproduction has long been recognised by zoo biologists, and people who work with animals often describe their different character traits (Powell & Svoke, 2008; Watters & Powell, 2012). Yet it is only recently that

the quantitative assessment of personality has been used to investigate some of the challenges faced in zoo animal breeding, management and welfare, and this developing field has provided new avenues of investigation into welfare assessment and the reproductive failure of individuals. Additionally, several authors identified the need for zoo animal personality assessment to be incorporated into existing zoo management practices (McDougall *et al*., 2006; Whitham & Wielebnowski, 2009, 2013; Watters & Powell, 2012). However there has been no published synthesis of the findings of animal personality research carried out in zoos, except for Tetley and O'Hara (2012), which is based on information presented in this section.

Hill and Broom (2009) emphasised the importance of taking individual differences into account when assessing animal welfare, and Whitham and Wielebnowski (2009) advocated the use of keeper ratings to regularly monitor the welfare of individuals. Indeed, research by King, Weiss and colleagues (Weiss *et al*., 2002; King & Landau, 2003; Weiss *et al*., 2006, 2009) has provided evidence that welfare (or 'subjective well-being') is related to personality in great apes. King and Landau (2003) found that keeper-rated subjective well-being was positively correlated with dominance in chimpanzees, and Weiss *et al*. (2006) found positive associations between subjective well-being, agreeableness and extraversion and a negative association between well-being and neuroticism in orang-utans. A recent study by Gartner and Weiss (2013b) also uncovered links between well-being and personality in captive Scottish wildcats (*Felis sylvestris grampia*).

Research into zoo animal personality has shown that zoo keepers are able to reliably rate animal personality traits, and that these ratings are valid and related to behaviour. The ability of keepers to reliably assess animal personality has been likened to the use of proxy informants in human clinical decision-making (Meagher, 2009; Whitham & Wielebnowski, 2009), where patients themselves are unable to communicate. Thus, knowledge of animal

personality has the potential to inform important management decisions relevant to breeding and welfare.

2.7.1. Personality and captive breeding: individual breeding success

One focus of recent research into zoo animal personality has been the effect of personality on individual breeding success. In their study of black rhinoceros breeding success and environmental variables, Carlstead and her colleagues (Carlstead, Fraser *et al*., 1999) found that zoos with larger rhino enclosures were more successful in breeding black rhinoceros, and 'dominance' scores were lower for males housed in larger enclosures. In a separate study, Carlstead, Mellen *et al*. (1999) found that dominance scores for males were negatively correlated with individual breeding success, and dominance scores for females were positively correlated with breeding success. In addition, the number of births per year spent together was higher in pairs of rhinos consisting of a submissive male and a dominant or aggressive female (Carlstead, Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999). Taken together, these results suggest that the optimum conditions for breeding black rhinoceros in captivity include large enclosures, which facilitate submissive behaviour in males, which in turn affects pair compatibility.

Powell *et al*. (2008) discovered a relationship between 'shyness' and socio-sexual behaviour in female pandas. This study is of particular interest because the authors used novel object and scent tests to assess the personality of the pandas, then compared these results to keeper ratings of socio-sexual behaviour. They found that females scoring highly on the 'shy' personality component were judged by their keepers to display fewer socio-sexual behaviours than females that were more 'confident' or 'bold'. This study also revealed that access to den sites within enclosures and interaction between keepers and pandas resulted in lower shyness scores. The authors were therefore able to recommend simple measures to reduce shyness and

increase socio-sexual behaviour, including increased keeper-panda interactions, which in turn could improve the reproductive success of female pandas (Powell *et al*., 2008).

The results of some zoo animal personality studies have led researchers to make recommendations to reduce fearfulness in order to improve reproductive success (e.g. Powell *et al*., 2008) and, since personality is heritable (Weiss *et al*., 2000; Drent *et al*., 2003), there is a danger that artificial selection is occurring for traits that predispose adaptation to a captive environment. Those same traits might be detrimental to survivorship of individuals in reintroduction programmes (McDougall *et al*., 2006). There is, therefore, an emerging tension concerning the relationship between personality and fitness in wild and captive animals. In captivity, fearfulness appears to be a predictor of reduced reproductive success (Wielebnowski, 1999; Powell *et al*., 2008; Smith & Blumstein, 2008) and chronic stress, characterised by increased faecal corticoid concentrations (Wielebnowski, Fletchall *et al*., 2002). Conversely, fearful individuals in the wild are often more likely to avoid predators and their chances of survival are therefore enhanced (Bremner-Harrison *et al*., 2004; Watters & Meehan, 2007, but see Réale & Festa-Bianchet, 2003). Systematic monitoring of personality in captivity could provide important insights into the effects of captive breeding and selection (McDougall *et al*., 2006).

2.7.2. Personality and captive breeding: pair compatibility

To maintain the genetic health of captive populations, recommendations for breeding pairs are made on the basis of kinship (Wedekind, 2002; Ballou *et al*., 2010; Asa *et al*., 2011). However, individuals that are a good genetic match for one another may not necessarily produce offspring and behavioural incompatibility is often cited for the failure of a recommended pair to breed successfully (Snyder *et al*., 1996; Carlstead, Mellen *et al*., 1999; Augustus *et al*., 2006; McDougall *et al*., 2006; Freeman *et al*., 2009; Lees & Wilcken, 2009).

This often results in an increased number of costly, time-consuming animal transfers, which can cause unnecessary distress to the individuals being moved (Wells *et al*., 2004; Lees & Wilcken, 2009; Asa *et al*., 2011). Indeed, Wells *et al*. (2004) reported elevated cortisol levels in cheetahs following transfer between institutions. Investigation into animal personality can shed light on the combination of personalities that might compose a successful breeding pair, and reduce the need for animal movements.

Personality may be linked with sexual selection (Both *et al*., 2005; Spoon *et al*., 2006; Schuett *et al*., 2010, 2011) and some studies in birds have begun to explore this link. Spoon *et al*. (2006) considered pairs of cockatiels (*Nymphicus hollandicus*) to be behaviourally compatible if they showed frequent affiliative behaviours, close proximity and little aggression. Compatible pairs showed greater co-ordination in parental care and raised more chicks to independence than pairs with low behavioural compatibility. In their study of personality and reproductive success in great tits, Both *et al*. (2005) characterised adults as either fast or slow explorers. They found that the offspring of pairs with extreme personalities, either two fast explorers or two slow explorers, were in better condition than the offspring of pairs consisting of one fast and one slow explorer. This may have been due to better co-operation by parents with similar personality types (Both *et al*., 2005). Likewise, Schuett *et al*. (2011) found that pairs of zebra finches (*Taeniopygia guttata*) with similar personality profiles raised healthier chicks than pairs whose personality profiles did not match. These finches were more exploratory and aggressive. Personality traits such as aggression and boldness may signal mate quality; the personality of a male might indicate his strengths as a parent, and females may choose mates on this basis (Schuett *et al*., 2010, 2011).

Little is currently known about the effects of personality combinations on the reproductive success of zoo mammals, despite the findings of Carlstead and her colleagues (Carlstead, Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999) that personality is a good

predictor of pair compatibility in black rhinoceros. Previous research has focused on species in which males and females form long-term pair bonds and co-operatively rear their offspring (Both *et al*., 2005; Spoon *et al*., 2006; Schuett *et al*., 2010, 2011). Studies of animals with other mating systems and behaviours will be useful in understanding further the link between personality and breeding success. Experimental studies in which the personality combinations of foster parents are manipulated (e.g. Schuett *et al*., 2011) can be used to inform zoo researchers about the potential for pair compatibility to influence reproductive success. However such manipulations are not possible in the zoo environment, so further research in this area will remain retrospective in its analysis of successful breeding pairs.

2.7.3. Personality and social groups

Since personality affects the compatibility of breeding pairs, it follows that the personalities of individuals within a social group can affect the social compatibility, stability and success of that group (Hessing *et al*., 1994; Sapolsky & Share, 2004; Sih & Watters, 2005; Watters & Meehan, 2007; Miller & Kuhar, 2008; Michelena *et al*., 2009; Freeman *et al*., 2010b; Massen & Koski, 2014). Thus, the assessment of personality can be used to inform decisions about which individuals could be placed together when planning the introduction of individuals into social groups (Stoinski, Lukas *et al*., 2004; Kuhar *et al*., 2006; Powell & Svoke, 2008).

The effects of personality on social group behaviour have been demonstrated in previous research. Sih and Watters (2005) investigated the effects of male behavioural type on group behaviour in water striders (*Aquarius remigis*). Groups containing hyper-aggressive males showed reduced reproductive activity, because these males harassed females and drove them out of the group. In their study of grazing behaviour in sheep (*Ovis aries*), Michelena *et al*. (2009) found that bold individuals were more likely to move to an alternate foraging patch

than shy individuals, when increased group size resulted in increased competition. The authors suggested that a mix of bold and shy individuals within a social group could contribute to group success, because the exploratory tendencies of bold individuals allow the discovery of new resource sites, whilst the tendency of shy individuals to remain close to conspecifics assists with maintaining group cohesion (Michelena *et al*., 2009). Similarly, a study of barnacle geese (*Branta leucopsis*) suggested that movement patterns of social groups can be affected by the personalities of group members (Kurvers *et al*., 2009). Kurvers and his colleagues found that the probability of an individual's arrival at a food patch was affected not only by the personality of the individual but also the personality of its companion (Kurvers *et al*., 2009). This notion was also discussed by Watters and Meehan (2007), who suggested that individuals of different personalities might fulfil different roles within a social group. Thus, the success of a social group could depend upon the combination of personalities present in the group.

A few zoo-based studies have investigated the effects of personality on social group cohesion. In their assessment of gorilla (*Gorilla gorilla*) personality in North American zoos, Gold and Maple (1994) described four factors of gorilla personality: 'extroverted', 'dominant', 'fearful' and 'understanding' (the Gorilla Behaviour Index, or GBI), and suggested that their instrument for rating gorilla personality could be used to inform management decisions. However, due to the small number of individuals for which behavioural data were collected, few correlations between these personality factors and behaviour were observed. Kuhar *et al*. (2006) attempted to validate the GBI and reassessed 119 male gorillas, collecting behavioural data on a subsample of 25 individuals at seven zoos. Their results indicated a stronger relationship between the GBI and observed behaviours. Furthermore, the understanding factor was related to social housing conditions, as males scoring highly on this factor were more likely to be housed in social groups, displaying high

rates of affiliative behaviour and little contact aggression, whilst solitary males that had been removed from social groups due to frequent instances of aggression scored lower on the understanding factor (Kuhar *et al*., 2006). This result raises the question of cause and effect; it is possible that solitary gorillas scored lower on this dimension because they were housed alone. However the authors argued that, in either case, low scores on the understanding factor appear to be predictive of those gorillas that might benefit from solitary housing (Kuhar *et al*., 2006). In addition, the authors reported two instances of the successful introductions of juvenile male gorillas to a silverback male. In both cases, the silverbacks scored highly on the understanding personality factor.

Similarly, Massen and Koski (2014) investigated the effects of personality on chimpanzee friendships. Friendships were characterised by time spent sitting in contact, and were related to small absolute differences between individuals in sociability and boldness. Thus, the personalities of friends were more similar than the personalities of non-friends. The authors hypothesised that homophily in boldness and sociability within non-kin friendships is adaptive, because it may enhance partner reliability in co-operative activities such as grooming (Massen & Koski, 2014).

Murray (1998) collected personality ratings for 59 chimpanzees housed at three UK zoos, and investigated the effect of social group size on personality. She found that chimpanzees in larger groups consisting of seven or more individuals were rated as more ‘sociable’, ‘curious’ and ‘playful’, and less ‘solitary’ and ‘slow’ than those housed in pairs or trios. This may have been due to the increased social complexity afforded by living in a large group, and a greater variety of social partners with which to interact. Murray (1998) also argued that infants raised in large social groups benefit from increased social contact at an early age. The results of this study highlighted the importance of providing captive

chimpanzees with an optimum social environment in order to ensure good welfare (Murray, 1998).

Freeman and her colleagues (Freeman *et al*., 2004, 2009, 2010a, 2010b) used information obtained from keeper questionnaires to investigate relationships between social behaviour, dominance status and ovarian activity in captive Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. In this body of work, the term *temperament* is used to describe social behaviour and dominance, and the results have shown that elephant keepers are able to reliably rate the behaviour of female African and Asian elephants and predict the social rank of elephants in their care (Freeman *et al*., 2010a, 2010b). Keeper ratings of social behaviour correlated strongly with direct observations of social interactions among African elephants (Freeman *et al*., 2010b) and females rated as dominant by their keepers were significantly more likely to approach, push and displace other elephants in the herd (Freeman *et al*., 2010a). Freeman *et al*. (2004) suggested that a female's personality may determine her social rank, since more aggressive females were more likely to be dominant. When viewed alongside the findings of Freeman *et al*. (2009), that dominant females were more likely to show ovarian acyclicity, the results of this research illustrate how keeper ratings could be used to further our understanding of the effects of individual differences in personality on social group behaviour and reproductive success among socially housed mammals.

2.8. Felid personality

In their recent review of felid personality studies, Gartner and Weiss (2013a) found only 21 published studies and 17 of those focused on the domestic cat (*Felis silvestris catus*). In a similar review of zoo animal personality research, over half of the reviewed papers (53%) focused on primates, and felid species were the subject of only five studies (Tetley & O'Hara, 2012). Personality has been previously assessed in five species of zoo-housed felids: cheetahs

(Wielebnowski, 1999; McKay, 2003; Baker & Pullen, 2013); clouded leopards (*Neofelis nebulosa*: Wielebnowski, Fletchall *et al*., 2002; DeCaluwe *et al*., 2013); Scottish wildcats (Gartner & Weiss, 2013b); snow leopards (Gartner & Powell, 2012) and Bengal tigers (*Panthera tigris tigris*: Phillips & Peck, 2007). Given the important role of personality in animal welfare, there is a need for felid personality to be investigated further.

Felid personality has been previously described by up to eight dimensions, broadly defined as: 'sociable'; 'dominant'; 'curious'; 'active'; 'aggressive'; 'calm'; 'timid' and 'excitable' (Gartner & Weiss, 2013a). Although different researchers use varying terms to describe felid personality, these dimensions appear to replicate across different felid species. Baker and Pullen (2013) found a sociability dimension in cheetahs, with high positive loadings on the trait 'playful'. Fearfulness has been described in a number of species, including cheetahs (Wielebnowski, 1999) and snow leopards (Gartner & Powell, 2012). Wielebnowski (1999) found a dimension labelled 'tense-fearful' in cheetahs. Individuals scoring highly on this dimension were rated as more insecure, tense, fearful of conspecifics and fearful of people, and less self-assured. Similarly, Gartner and Powell (2012) found a 'timid/anxious' dimension in snow leopards, consisting of the traits 'anxious', 'fearful', 'insecure' and 'tense'.

Previous research into felid personality has focused on the relationships between personality and breeding success, adrenal activity and subjective well-being. DeCaluwe *et al*. (2013) assessed the personalities of male clouded leopards, and correlated the results with behavioural observations and faecal glucocorticoid levels in order to assess anxiety and aggression. The results showed that individuals rated as more anxious by their keepers had higher glucocorticoid concentrations and displayed more behaviours indicative of fearfulness (e.g. hiding behaviour) than individuals rated as calm. An earlier study, carried out by Wielebnowski and colleagues (Wielebnowski, Fletchall *et al*., 2002), uncovered links

between fearfulness and pacing behaviour, self-injuring behaviour and faecal corticoid concentrations. Taken together, these results indicated chronic anxiety within the captive clouded leopard population, evidenced by keeper ratings, behavioural observations and hormone analyses. Recommendations arising from these studies for improving the welfare of clouded leopards included the provision of elevated areas and increased enclosure height (Wielebnowski, Fletchall *et al*., 2002), and the use of personality assessment to predict appropriate male-female pairings and reduce intra-specific aggression (DeCaluwe *et al*., 2013), which is a barrier to successful captive propagation in this species (Law & Tatner, 1998; Wielebnowski, Fletchall *et al*., 2002; DeCaluwe *et al*., 2013).

In their study of Scottish wildcat personality and subjective well-being, Gartner and Weiss (2013b) found three personality dimensions, labelled 'dominance', 'agreeableness' and 'self-control'. Keepers were also able to reliably rate the wildcats on a subjective well-being questionnaire, and well-being was linked with the self-control personality dimension. Animals with high scores on the self-control dimension were judged by their keepers to derive pleasure from social interactions and have balanced positive and negative moods. Thus, higher self-control was related to increased well-being. Gartner and Weiss (2013b) argued that this link between personality and subjective well-being could have implications for health and welfare.

2.8.1. Cheetah personality

Wielebnowski (1999) obtained ratings on 18 behavioural characteristics for 44 cheetahs housed at four breeding facilities in North America. Behavioural observations were then conducted during a mirror-image stimulation test, in which 41 of the cheetahs were presented with a mirror and their reaction to their mirror image was recorded, including their latency to approach the mirror and the frequency of growling and hissing. Principal Components Analysis (PCA) revealed three components of cheetah personality: 'tense-

fearful'; 'vocal-excitable' and 'aggressive'. High scores on the tense-fearful component were positively correlated with the amount of time taken to approach the mirror, and cheetahs rated as more aggressive were significantly more likely to growl, hiss and stare at their mirror image. When the components of personality were examined in relation to breeding success, the results revealed that individuals who had bred successfully scored significantly lower on the tense-fearful component than non-breeders. This study was one of the first published papers to investigate the effects of individual differences on reproductive success in a zoo-housed species, and demonstrated the potential for further investigation into cheetah personality. The study provided the first evidence that personality in cheetahs can be reliably assessed using keeper ratings, and that these ratings are valid and related to behaviour. Despite this, little further research has been published into the effects of personality on the behaviour and reproductive success of captive cheetahs.

In a UK study, McKay (2003) also reliably assessed cheetah personality using keeper ratings at nine zoos, but found no differences in the personality scores of breeders and non-breeders. The personality of 41 individuals was assessed and three components of personality were identified: 'aggressiveness' 'inquisitiveness' and 'flehmen/faecal mark/sleep'. Whilst the underlying meaning of the third component was unclear, it was likened to fearfulness. The aim of McKay's study was to compare the personality and breeding success of individuals with environmental factors and husbandry routines, and an individual's breeding success was only analysed for the time spent at their current institution at the time of the study. This resulted in a small number of breeding individuals within the sample (two males and five females) that, unlike Wielebnowski's (1999) study, did not allow an effect of personality on breeding success to be detected (McKay, 2003). Thus, there is a need for further investigation into the links between personality and breeding success in this species.

A recent study by Baker and Pullen (2013) attempted to correlate cheetah personality with husbandry variables. Keeper ratings were received for 34 cheetahs housed at seven UK zoos and three components of personality were identified, labelled by the authors as 'dominance', 'sociability' and 'keeper-directed sociability'. Animals scoring highly on the dominance dimension were considered to be more aggressive and assertive than animals with low dominance scores, and dominance scores were lower if keepers entered the cheetah enclosure on a regular basis. Keeper-directed sociability was characterised by high scores on the trait 'friendly to you' (friendly to keepers) and low scores on the trait 'aggressive to you' (aggressive to keepers). However, no differences in keeper-directed sociability were reported for animals whose keepers entered the enclosure and for those whose keepers did not enter the enclosure. High sociability scores were indicative of animals scoring highly on the trait 'playful' and low scores on the trait 'timid/shy'. Males were significantly more sociable than females, which may reflect the social tendencies of wild males and the solitary nature of wild females. However, the males in the study were group-housed and the females were singly-housed, and the authors acknowledged that this finding may have resulted from the animals' housing situation. Reproductive success was not investigated in the study, due to the small number of breeders in the sample (Baker & Pullen, 2013).

Cheetah personality has previously been successfully assessed, and may prove to be a valuable tool for captive cheetah care providers. However, further investigation into the effects of personality on cheetah behaviour has yet to be undertaken. Clearly, there is a need for the personality of a large sample of individuals to be surveyed if links between personality and breeding success are to be explored further. The present research builds on previous work (Wielebnowski, 1999; McKay, 2003; Baker & Pullen, 2013) by assessing the personality of 120 cheetahs housed in the UK and beyond, and investigating links between personality, pair compatibility and social group cohesion.

2.9. Research aim and objectives

Despite continued breeding efforts, the captive cheetah population is not self-sustaining. This is detrimental to cheetah conservation and might indicate underlying welfare concerns. Several authors identified the need for further research into the behaviour and management of captive cheetahs (Laurenson *et al*., 1992; Caro, 1993; Lindburg *et al*., 1993; Wielebnowski, 1996; Wielebnowski & Brown, 1998; Wielebnowski, Ziegler *et al*., 2002; Crosier *et al*., 2007; Bauman *et al*., 2010), yet little effort has so far been made to investigate captive cheetah behaviour in detail. The lack of published studies into captive cheetah social behaviour is particularly surprising, since field observations have revealed a complex and unusual social system in wild cheetahs.

2.9.1. Aim

Given that appropriate social group housing can greatly enhance the welfare and reproductive success of captive animals, and that individuals vary in their responses to the captive environment, this research investigates in detail the behaviour, spatial association and personality of captive cheetahs housed in different social groups. The aim of the research is to determine the effects of social group housing and personality on the behaviour and reproductive success of captive cheetahs.

2.9.2. Objectives and hypotheses

Objective 1

- *To compare the behaviour and activity of captive cheetahs housed in natural and unnatural social group types.*

Appropriate social group housing is essential for animal welfare (Morgan & Tromborg, 2007; Price & Stoinski, 2007). It is hypothesised that cheetahs housed in natural social groups (i.e. those group-types that have been observed in wild populations) will display species-specific social behaviours; and those housed in unnatural groups (i.e. those that have not been observed in wild populations) will exhibit increased pacing behaviour, typically associated with stress and reduced welfare (Wielebnowski, Ziegler *et al*., 2002). Further, it is predicted that institutions housing their cheetahs in natural social groups will have better reproductive success than those housing their cheetahs in unnatural social groups (Mellen, 1991).

Objective 2

- *To investigate spatial association in group-housed cheetahs.*

Evidence from the wild suggests that coalitions of males remain in close proximity to one another, move around their territories together, and display affiliative behaviours (Caro, 1994; Gottelli *et al*., 2007). There is also evidence that stronger associations are formed between related individuals than between unrelated individuals (Caro, 1994; Ruiz Miranda *et al*., 1998). In contrast, wild females are solitary and adult females do not form social groups (Caro, 1994; Wielebnowski, Ziegler *et al*., 2002; Terio *et al*., 2003). Thus, it is hypothesised that males housed in groups in captivity will maintain close proximity to one another, related males will be more closely associated than unrelated males, and that weak associations will be found among group-housed captive females.

Objective 3

- *To explore the relationship between cheetah personality profiles, behaviour and breeding success.*

Previous research has suggested that personality may be correlated with breeding success (Wielebnowski, 1999), and that the individual personalities in a breeding pair or social group might influence the success of that pair or group (Murray, 1998; Carlstead, Mellen *et al*., 1999; Kuhar *et al*., 2006). Thus, information about the personality of an individual could be invaluable to staff at institutions involved in co-ordinated captive breeding programmes. It is hypothesised that keepers will be able to reliably rate cheetah personality, and that their ratings are valid and related to behaviour (Wielebnowski, 1999; McKay, 2003; Baker & Pullen, 2013). Further, it is predicted that individuals that have bred successfully will be rated as less fearful by their keepers than those that have not bred successfully (Wielebnowski, 1999), and that individuals housed in social groups will score highly on personality traits related to sociability (Murray, 1998; Kuhar *et al*., 2006). In addition, this research will investigate pair compatibility in cheetahs by comparing the personality profiles of successful and unsuccessful breeding pairs.

2.10. Conclusion

This chapter presented a critical review of the literature in the fields of cheetah conservation, biology, ecology and behaviour. It has shown that the social environment is critical for the welfare and reproductive success of captive animals. Field observations have revealed a complex social system in wild cheetahs, yet captive cheetah social behaviour is an understudied topic. In addition, individuals vary in their responses to the captive environment and animal personality can also have implications for welfare and reproductive success.

Information drawn from the literature was used to formulate the research aim, objectives and hypotheses. The following chapter presents background information on the

methods adopted to address the research aim and objectives, and the justification for selecting the chosen methods.

3. Methods

3.1. Introduction

A number of methodological approaches were required to address the research objectives. The most appropriate method to determine the effects of social group housing on the behaviour of captive cheetahs housed in different social groups was behavioural observation (Objective 1). Geographic Information Systems (GIS) and indices of association were used for Objective 2, which required the analysis of a large spatial dataset. The use of a GIS enabled spatially referenced information on cheetah social interactions to be analysed in detail and facilitated the calculation of indices of association, which quantified relationships among group-housed individuals. As Objective 3 investigates links between personality, behaviour and reproductive success across the cheetah EEP (European Endangered Species Breeding Programme), a survey of cheetah keepers was undertaken to collect information on cheetah personality.

This chapter provides background information on the methods used to collect behavioural data (Section 3.2), including a discussion of the use of indices of association (Section 3.3) and GIS (Section 3.4) in animal behaviour research. A review of data collection methods for assessing zoo animal personality is presented in Section 3.5.

3.2. Behavioural observations

This research uses scan sampling and instantaneous recording to collect data on the behaviour of cheetahs housed in different social groups. Observations of behaviour provide information about many different indicators of animal welfare (Lindburg & Fitch-Snyder, 1994; Mench & Mason, 1997; Mallapur, 2005; Watters *et al*., 2009), without the need for invasive procedures. The behaviour of captive individuals can indicate whether they are in the

correct physical and social environment, or receiving an appropriate diet (Lindburg & Fitch-Snyder, 1994; Mallapur, 2005; Watters *et al*., 2009; Crockett & Ha, 2010), and changes in behaviour can indicate changes in physiology, health and welfare (Mench & Mason, 1997; Watters *et al*., 2009). Indeed, Watters *et al*. (2009) advocated the use of behavioural monitoring as a component of standard animal care procedures.

The majority of zoo research studies involve behavioural observations (Finlay & Maple, 1986; Stoinski *et al*., 1998; Mallapur, 2005; Rees, 2005; Watters *et al*., 2009). In a zoo setting, behavioural observations have been used to evaluate the effects of environmental enrichment (Carlstead *et al*., 1991; McPhee, 2002; Bashaw *et al*., 2003; Swaisgood & Shepherdson, 2005; Quirke & O'Riordan, 2011), monitor the introductions of individuals into new social groups (Seres *et al*., 2001; Abelló & Colell, 2009) or mixed-species exhibits (Wojciechowski, 2004; Dorman & Bourne, 2010), and to monitor the introductions of males and females for breeding (Law & Tatner, 1998).

Common methods for observing behaviour include focal animal sampling and scan sampling (sampling rules), alongside instantaneous or continuous recording (recording rules). In focal animal sampling, one individual is selected for observation. Continuous recording is often coupled with focal animal sampling, where all the behaviours performed by the focal animal, and their duration, are recorded for a pre-determined time period defined by the researcher (Altmann, 1974; Martin & Bateson, 2007; Crockett & Ha, 2010). The length of the sampling period will depend upon the research question, and is often limited by observer fatigue (Altmann, 1974). It is difficult to concentrate on one individual for a prolonged period, and fatigue can affect the accuracy of recordings. Continuous recording results in detailed information about the behaviour of the focal animal, and can enable infrequent behaviours or behaviours of short duration to be investigated (Martin & Bateson, 2007; Crockett & Ha,

2010). However, analysis of continuous records can be time consuming and focal animal sampling, by definition, only focuses on individual animals, rather than groups.

In scan sampling, a whole group of animals is observed simultaneously. Instantaneous recording is commonly used alongside scan sampling, and the behaviour of all individuals is recorded at the instant ending of a pre-determined sampling interval; for example every minute (Altmann, 1974; Martin & Bateson, 2007; Crockett & Ha, 2010). Instantaneous recording is the easiest method to use for estimating the percentage of time spent by animals engaged in specific activities (Crockett & Ha, 2010). However, it does not result in exact durations of behaviour, and infrequent behaviours or those of short duration are often missed unless they occur at the instant of recording. In practice, researchers often adopt more than one method, and different sampling rules and recording rules can be used in different combinations.

The methods used to observe and record behaviour, along with the time frame allocated for behavioural observations, can dramatically influence results. Sampling regimes should be designed to enable data that are representative of actual behavioural patterns to be collected (Crockett & Ha, 2010). If specific behaviours are of interest, preliminary observations can be conducted to identify appropriate observation times. For example, in a study of the terrain preferences for play behaviour in young Siberian ibex (*Capra ibex sibirica*), Byers (1977) conducted 50 hours of preliminary observations to identify the times of day when play behaviour was most common. Systematic data collection for the study was then conducted between the hours of 0500 and 0700, and 1900 and 2115. If the study focuses on general activity patterns, observation sessions should be balanced throughout the day (e.g. Stoinski, Kuhar *et al*., 2004) or, preferably, take place over whole days to provide a true estimate of activity patterns.

The amount of time spent observing behaviour may influence the conclusions of behavioural studies. Quirke and O'Riordan (2013) used five different methods to collect behavioural data on captive cheetahs following environmental enrichment. Each of the five methods was designed to simulate varying degrees of sampling effort and ranged from fifteen minutes to two hours of scan sampling per day, over sixteen days. Perhaps unsurprisingly, no significant differences in behaviour were found between baseline and enrichment days when only 15 minutes of observation were carried out each day, whereas significant differences in behaviour were found when two hours of observation were carried out. The authors went on to discuss the results in relation to assessing the efficacy of environmental enrichment, and highlighted the fact that whilst the enrichment did result in changes in the behaviour of the animals (Quirke & O'Riordan, 2011), these changes would not be detected with reduced sampling effort and this would lead to the erroneous conclusion that the enrichment was not effective (Quirke & O'Riordan, 2013).

Margulis and Westhus (2008) pointed out that systematic data collection is often not possible due to time constraints. This is particularly the case in zoo-based research, where husbandry routines or the needs of the animals may limit the time that can be spent by researchers observing behaviour. Margulis and Westhus (2008) used different sampling regimes to record the behaviour of polar bears. They found no significant differences in the activity budgets resulting from varying degrees of sampling effort, including 32 hours of scan samples every 30 minutes, six hours of scan samples every ten minutes, and scan samples taken once every hour during 22 keepers' working days. However, significant differences were found in the occurrence of social interactions, which were only recorded using the first sampling regime. The authors argued that limited sampling regimes can produce good measures of common behaviours. However, more time spent observing behaviour results in a

greater variety of behaviours observed (Quirke & O'Riordan, 2013) and more accurate information about activity and social interactions.

Since the present research investigates the behaviour of cheetahs housed in different social groups, and data on the behaviour of all group members were required, scan sampling and instantaneous recording were chosen over focal animal sampling and continuous recording. Detailed procedures for behavioural data collection are presented in Section 4.3 of Chapter 4. Briefly, recordings of the behaviour of all animals were made at 60-second intervals onto check sheets (Appendix 1) using a stopwatch. This method is suited to studies of social group behaviour because data are obtained simultaneously on the entire group. It also provides data on behavioural synchrony, which is not possible to obtain using focal animal sampling (Altmann, 1974). The short sampling interval resulted in an estimate of the percentage of time spent by all animals in each group performing specific behaviours (Altmann, 1974), whilst allowing time for the behaviour of all individuals to be recorded before the onset of the next sampling point. To record social interactions that may be infrequent or of short duration, and thus missed by instantaneous recording, an all-occurrences method (Altmann, 1974) was used alongside the instantaneous recording rule. All occurrences of social interactions were recorded, whether they occurred at the instant of recording, or between recording intervals (*sensu* Margulis & Westhus, 2008). To enable data that are representative of actual behavioural patterns to be collected, behaviour was observed all day, during zoo opening hours. Data collection visits to participating zoos were made throughout the year, to allow for potential seasonal variation in behaviour.

3.3. Indices of association

Social behaviour may be evaluated and quantified by way of an index of association. In the present research, a simple ratio index of association was used (Ginsberg & Young,

1992). Indices of association were originally developed by ecologists to analyse how often plant species were found in proximity to one another (Southwood, 1968) but have also been used since at least the 1970s to quantify social relationships between individual animals living in groups (e.g. lions: Schaller, 1972; spider monkeys (*Ateles geoffroyi*): Chapman, 1990; spotted hyenas (*Crocuta crocuta*): Szykman *et al*., 2001; Spix's disc-winged bats (*Thyroptera tricolor*): Vonhof *et al*., 2004; cheetahs: Chadwick *et al*., 2013). Association indices assume that physical proximity is an indication of social affiliation (Bejder *et al*., 1998; Knobel & du Toit, 2003) and calculate the proportion of time individuals in dyads are seen together (Whitehead & Dufault, 1999; Whitehead, 2008a). Possible values of an index of association range between zero and one: a score of zero indicates two individuals are never seen together, a score of one that two individuals are always seen together (Bejder *et al*., 1998; Martin & Bateson, 2007). This remains a useful technique despite the growing popularity of social network analysis. Although sociograms can be drawn for dyads (e.g. Chadwick *et al*., 2013), detailed social network analysis is only appropriate for larger groups, where extensive observations of interactions between individuals have been made (Whitehead, 2008b, 2009; Perreault, 2010). Indeed, Perreault (2010) demonstrated that parameters such as mean path length (the mean distance between individuals in the network) and the number of components (groups of interconnected individuals that are not connected to the rest of the network), were affected by the number of edges (connections between individuals) in a sample, when the total number of individuals in the network was held constant. It should be noted here that Perreault (2010) considered his theoretical population of 125 individuals to represent a small network.

Four commonly used association indices are presented in Table 3.1. Ginsberg and Young (1992) recommended the general use of the simple ratio index. Use of this index is based on four assumptions:

"1. Recorded association is a symmetric one-zero measure of whether the members of a dyad are or are not associated in a sampling period.
2. Recorded associations are accurate.
3. If one individual is identified in a sampling period, then all its associates are identified.
4. Members of a dyad are equally likely to be identified whether they are associated or not associated."

(Whitehead 2008a, p. 98)

If these assumptions are not met, the simple ratio index will be biased and a more appropriate index should be selected.

Table 3.1. Commonly used association indices. Adapted from Whitehead (2008a).

Index	Formula
Joint occurrences	x
Simple ratio	$\frac{x}{x + y_{AB} + y_A + y_B}$
Half-weight	$\frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$
Twice-weight	$\frac{x}{x + 2y_{AB} + y_A + y_B}$

x: number of sampling periods when animals A and B are observed together; y_A: number of sampling periods when only A is observed; y_B: number of sampling periods when only B is observed; y_{AB}: number of sampling periods when A and B are observed not associated.

In addition to the simple ratio index, Whitehead (2008a) described a further six association indices, which can be used when the assumptions of the simple ratio index are not met. In studies of wild populations, association is often defined on the basis of group membership. Thus, members of a dyad may be more likely to be identified when they are together or more likely to be identified when they are apart, and association and identification

are therefore linked (Whitehead, 2008a). Cairns and Schwager (1987) recommended the use of the twice-weight index when pairs are more likely to be identified when they are together, and the half-weight index when pairs are more likely to be identified when apart. However in studies of captive animals, identification of individuals is not based solely on group membership and all individuals and their associates can be observed in every sampling period (e.g. Knobel & du Toit, 2003; Romero & Aureli, 2007).

It is necessary for researchers to define what constitutes an association, and associations between individuals are often defined spatially (Whitehead & Dufault, 1999). In their review of techniques for analysing vertebrate social structure, Whitehead and Dufault (1999) found large variation in the distances between individuals which constituted an association. Some authors considered animals to be associated if they were within 1m of each other (e.g. captive common marmosets (*Callithrix jacchus*): Koenig & Rothe, 1991), and in other studies animals were considered to be associated if they were within 500m of each other (e.g. wild giraffes (*Giraffa camelopardalis*): Leuthold, 1979). Animals may also be considered to be associating when they are within a certain number of body lengths of one another (e.g. Knobel & du Toit, 2003; Gusset *et al*., 2006), or when they are observed in the same subgroup (e.g. Chapman, 1990). In their study of social dynamics among relocated elephants, Pinter-Wollman *et al*. (2009) defined individuals as associating if they were observed within 500m of one another within a 2-hour time period. The study focused on social group behaviour in a novel habitat, and the authors argued that the definition of association accounted for the communicative capabilities of elephants to obtain information about the environment from vocalising conspecifics. The definition of an association will depend upon the interactions and behaviours of the study species and the ease of observing individuals. However, Whitehead and Dufault (1999) pointed out the importance of selecting

an appropriate definition of association that corresponds to the behaviour of the animals being studied.

Szykman *et al*. (2001) investigated whether male mate choice occurred in free-living spotted hyenas. Twice-weight association indices were calculated for male-female dyads and animals were considered to be associating when both individuals were seen in the same observation session. Spotted hyena groups are matrilineal, and contain one or more immigrant males. The results of the study revealed that males were significantly more closely associated with high ranking females than low ranking females, and analysis of cub paternity showed that sires were closely associated with the mothers of cubs, particularly in the month leading to conception. The authors suggested that the association data demonstrated selective mate choice by male hyenas.

The potential problems of using an association index to investigate social structure in large communities of animals were highlighted by Chilvers and Corkeron (2002). Specifically, the identification of individuals within a given time period and study area may cause bias in the association data. Chilvers and Corkeron (2002) used a half-weight index of association to analyse association patterns in a community of bottlenose dolphins (*Tursiops aduncus*), in which 550 individuals could be identified. Different selection criteria for inclusion in the analysis were employed based on the number of times individuals had been sighted during the whole study. As the number of individuals included in the analysis increased, the proportion of zero association values also increased, from 31% when 20 individuals were included to 82% when 151 individuals were included. The authors recommended the use of other population characteristics alongside association indices, such as estimates of community size and the proportion of identifiable individuals within the community, to improve the accuracy of analyses of social structure.

3.3.1. Association in captive animals

Whilst the majority of studies using indices of association have been conducted on wild populations (Whitehead & Dufault, 1999), some authors have used association indices to investigate social behaviour in captive animals.

An association index was used by Knobel and du Toit (2003) to document the social structure of a pack of captive African wild dogs (*Lycaon pictus*). The results revealed that the pack was split into two subgroups, one containing dominant individuals and one containing subordinates. Given that social structure determines feeding activities in this species, with high ranking individuals dominating food consumption, information about the pack structure was then used to ensure that all individuals in the pack received an oral rabies vaccine.

Romero and Aureli (2007) observed associations in a group of zoo-housed ring-tailed coatis (*Nasua nasua*). Animals were considered to be associating when they were within 2m of each other, and the results suggested that two subgroups existed within the larger study group of thirteen individuals. Individuals within the subgroups remained closely associated, whilst associations between the subgroups were weak. In addition, affiliative interactions were more frequent within than between groups, and aggressive interactions were more frequent between than within the groups. Their study enabled the social structure of ring-tailed coatis to be observed in greater detail than had been previously been possible in wild studies, and demonstrated the value of collecting behavioural data on social interactions alongside spatial association data.

Association indices provide an estimate of the proportion of time animals are seen together. However, it is difficult to calculate how often individuals are observed associating together simply by chance (Martin & Bateson, 2007). At least one attempt has been made to take chance encounters into account in a wild population. Schülke and Kappeler (2003) calculated expected encounter rates between pairs of fork-marked lemurs (*Phaner furcifer*)

using a random gas model (Equation 3.1), where the expected frequency of encounter (f) is dependent on the density (p) of a species, the velocity of the animals (v), the group spread (s) and the distance criterion which defines association (d). This method, however, relies on variables that are difficult to measure, such as group spread (dispersion) and the velocity (rate of movement) of animals.

$$f = \frac{(4pv)}{\pi(2d + s)} \qquad \text{Equation 3.1}$$

The problem of chance associations is more pronounced in a captive environment, where the space available to animals is limited relative to the wild and associations can occur for reasons other than the animals choosing to be together; for example mutual attraction to a food source, or gathering at the entrance to indoor accommodation. Stoinski *et al*. (2001) found that captive western lowland gorillas (*Gorilla gorilla gorilla*) spent more time near the holding buildings in their exhibit than expected by chance. The problem is also evident in multi-zoo studies, where enclosure sizes (and shapes) vary across institutions, making direct comparison of association indices difficult. Despite the spatial confinement of captive animals rendering their free movement, relative to cage mates, potentially limiting, few attempts have been made to estimate – and thus control for – chance encounters for any species in captivity (but see Chadwick *et al*. (2013) and Chadwick *et al*. (under review), which are based on material presented in Chapter 5 of this thesis).

The present research uses the simple ratio index (Table 3.1; Ginsberg & Young, 1992) to investigate patterns of association in group housed cheetahs. Its use is justified in this instance, as the subjects of the study were captive animals and the assumptions that the measure of association is symmetrical (i.e. individuals are either associated or not associated), all individuals can be identified, and the identification of individuals does not depend on whether or not they are associated (Whitehead, 2008a) were met. Thus, the simple ratio index

gives an unbiased estimate of the proportion of time individuals were seen together (Ginsberg & Young, 1992; Whitehead, 2008a). Given that the index is a ratio of the total number of observations of two individuals, it is robust against differences in the number of observations between individuals (Wittemyer *et al*., 2005).

During extensive field observations of coalitions of wild male cheetahs in the Serengeti, Caro (1994) reported that coalition members remained within 5m of one another during the mid-day rest period (0930h to 1700h). Here, I applied that established distance criterion for affiliated individuals when quantifying associations. Thus, individuals were considered to be associating when the distance between them was 5m or less. To control for chance encounters, I devised a simple Monte Carlo simulation and used GIS software to generate random locations within spatially referenced images of cheetah exhibits. Information from the simulation was used to correct indices of association calculated from field observations (Chadwick *et al*., 2013).

3.4. The use of GIS in studies of animal behaviour

This research uses Geographic Information Systems (GIS) to investigate in detail the spatial association patterns of captive cheetahs housed in social groups. Geographic Information Systems allow the visualisation and analysis of geographic data, based on commonly referenced spatial locations (Bentley-Condit & Hare, 2007; Karanth *et al*., 2010). This requires information on animal locations to be obtained. In the field, animal location data are collected remotely (Brooks *et al*., 2008; Tomkiewicz *et al*., 2010) using Global Positioning System (GPS) technology (e.g. Wall *et al*., 2006; Coelho *et al*., 2007) or radio telemetry (e.g. Muntifering *et al*., 2006; Marker, Dickman *et al*., 2008).

The use of GIS in animal behaviour research has primarily focused on habitat selection and home range analysis in wild populations (Blake *et al*., 2001; Scholz & Kappeler,

2004; Muntifering *et al*., 2006; Bentley-Condit & Hare, 2007; Marker, Dickman *et al*., 2008; Hilborn *et al*., 2012). In many cases, the use of GIS has enabled the calculation of the home range size of species which range over vast areas, which would not have been possible using traditional field observations alone (Blake *et al*., 2001).

Scholz and Kappeler (2004) plotted GPS location data in a GIS to analyse home ranges and migration patterns in red fronted lemurs. Three of the four study groups demonstrated seasonal migration from their habitual home ranges when water resources became scarce. Similarly, Musiega and Kazadi (2004) used a GIS alongside radio tracking and remote sensing techniques to predict migration routes of wildebeest in east Africa. Their results revealed the influence of vegetation and terrain characteristics in the routes taken by wildebeest herds on their annual migration from the Serengeti in Tanzania to the Masai Mara in Kenya.

GIS techniques have been used to investigate the home range characteristics and habitat use of wild cheetahs. In a recent study, Hilborn *et al*. (2012) observed 295 cheetah hunts in the Serengeti and plotted their locations onto a map of the study area within a GIS. They found that stalking behaviour initiated near to a river was more likely to end in a chase, and suggested that vegetation cover near rivers assisted cheetahs in approaching prey undetected. This study linked spatial information with behavioural data to reveal complex interactions between habitat, predators and prey. Muntifering *et al*. (2006) found that cheetahs on Namibian farmlands preferred areas of high prey visibility and high grass cover. This study provided information about cheetah range use outside of protected areas, which may help to understand and mitigate human-cheetah conflict. If those areas which are most used by cheetahs are identified, farmers can take precautions against livestock losses and graze their animals elsewhere (Muntifering *et al*., 2006).

Field studies, by definition, focus on large areas of habitat. Yet GIS can also be used to investigate how captive animals make use of the space available to them, which can inform important management decisions regarding animal welfare. Blowers *et al*. (2012) used GIS in their study of enclosure use by Nile hippopotamus (*Hippopotamus amphibius*). The exhibit was divided into grid squares and each square was categorised according to water depth. Analysis of the locations of the animals within the GIS revealed that the distribution of animal locations was significantly different from random, and that the hippopotamus demonstrated selection for shallow water depths. Understanding how animals use the available space within enclosures can inform future planning and exhibit design (Blowers *et al*., 2012).

Leighty *et al*. (2009) monitored walking rates of seven female African elephants, housed at Disney's Animal Kingdom (Florida, USA), using GPS collars. The mean distance travelled by the animals equated to 3.68km per day, which is comparable with distances observed in studies of wild elephants under non-extreme environmental conditions (Leighty *et al*., 2009). A significant effect of enclosure size on walking rates was uncovered in this study: individuals housed in larger enclosures showed higher walking rates than those housed in smaller enclosures. The authors suggested that the complexity of the exhibit mimicked the habitat of wild elephants and promoted exploratory behaviour.

In a similarly conducted study, Leighty *et al*. (2010) used GPS collars to record the locations of five female African elephants, also housed at Disney's Animal Kingdom. Spatial analyses in a GIS revealed that dominant individuals used significantly more of the available space, and spent more time at the watering hole, than subordinate females. The results indicated the effects of social group dynamics on resource use, and the authors advised that valuable resources should be evenly distributed around enclosures to allow access for subordinate individuals (Leighty *et al*., 2010).

Bentley-Condit and Hare (2007) also found differences in space use according to social rank. Female olive baboons (*Papio anubis*) used particular areas of their enclosure for particular behaviours, for example feeding and resting, and the areas used for different activities varied among individuals. Further spatial analyses revealed that this clustering of space use was influenced by social group dynamics, as females of higher rank were found in different areas of the enclosure to females of lower rank.

There is, therefore, a recognised potential for the use of animal location data, analysed in a GIS, to investigate the spatial aspect of social group behaviour of captive animals. The present research uses GIS to investigate cheetah social behaviour in greater detail than has been achieved hitherto using similar techniques. Locations of group-housed individuals were recorded and imported into a GIS for spatial analyses. Rather than GPS collars, detailed, paper maps of cheetah exhibits were used to record the position of individuals within enclosures while simultaneously recording behavioural observations.

Collection of location data using GPS involves fitting collars to animals containing GPS receivers, which are programmed to record and store the location of the wearer at intervals defined by the researcher (Coelho *et al*., 2007; Brooks *et al*., 2008; Tomkiewicz *et al*., 2010). The availability of GPS technology has advanced the study of animal behaviour and ecology, however it does have limitations.

One problem inherent to GPS devices is spatial imprecision. Modern commercial GPS receivers used in wildlife tracking collars are consistently accurate to within 30m (Frair *et al*., 2010; Tomkiewicz *et al*., 2010), with a range of reported accuracies from 3m or more (Frair *et al*., 2010). D'Eon *et al.* (2002) placed GPS collars at fixed locations in mountainous terrain, and found that horizontal differences between recorded locations and true locations ranged from 5.9m to 30.6m. In a similar study, Lewis *et al*. (2007) placed 18 GPS collars at known test sites in the Purcell Mountains (Idaho, USA) and reported a mean location error of 14.3m.

In the present research, animals were defined as associating when the distance between them was 5m or less (Section 3.3.1, above), and the required precision of location data was greater than is currently provided by standard commercial GPS collars.

The problem of spatial imprecision is further exacerbated by habitat characteristics. GPS collars are limited by their ability to locate at least three satellite signals in order to make position recordings. Physical obstructions between the collar and the satellites can reduce the number of satellites available to the GPS receiver (D'Eon *et al*., 2002). Thus, the success of signal acquisition is affected by vegetation cover and terrain complexity (D'Eon *et al*., 2002; Lewis *et al*., 2007; Frair *et al*., 2010). Coelho *et al*. (2007) found that GPS collars worn by maned wolves (*Chrysocyon brachyurus*) made significantly more recordings in hours of darkness, when the wolves were active in open habitat, than in daylight hours, when the wolves were resting in dense undergrowth. Similarly, Blake *et al*. (2001) found a negative correlation between signal acquisition and vegetation density in their study of activity patterns of African forest elephants (*Loxodonta africana cyclotis*), and the signal acquisition in dense forest was less than 10%. In addition, in their review of potential errors associated with GPS data, Frair *et al*. (2010) reported measurement errors of 12-17m caused by vegetation cover, and errors of 10-13m caused by terrain complexity.

The final limitation which prevented the use of GPS collars in this research was the attachment of equipment to the study animals. Whilst GPS collars can be remotely programmed to release, allowing the researcher to collect the collar later, it is necessary to anaesthetise wild animals for the attachment of GPS collars (Caro, 1994; Davis *et al*., 1999; Brooks *et al*., 2008; Casper, 2009). This invasive procedure was not permitted by any of the participating zoos.

Given the reduced rate of GPS signal acquisition in densely vegetated or built-up areas, spatial imprecision and the need to anaesthetise animals, manually recording animal

positions onto enclosure maps was considered the most appropriate method for obtaining location data in this research. The advantages of this method over remote data collection using GPS collars are that the positions of the animals can be recorded in fine detail and the behaviour of the animals can be recorded at the same time as their locations within the exhibit.

The method of manually recording animal locations has been successfully implemented in previous studies of captive animals. In their study of enclosure use in large felids, Lyons *et al*. (1997) recorded the positions of individuals onto enclosure maps that were divided into 2m x 2m grid squares. Similarly, Lukas *et al*. (2003) recorded the locations of gorillas onto enclosure maps before dividing the map into three areas. They found that the gorillas' use of exhibit space increased following their introduction into a novel exhibit. Blowers *et al*., (2012) recorded hippopotamus locations onto a map of the exhibit. The map was divided into grid squares and the locations of the animals were recorded onto the map at 10-minute intervals. An aerial image of the exhibit was then imported into GIS software and the animal locations were manually placed onto the exhibit image in the GIS. Bentley-Condit and Hare (2007) also recorded the point locations and routes of captive female olive baboons onto drawings of the enclosure, before digitising the drawings into a GIS.

Procedures for the collection and analysis of location data in the present research are described in detail in Section 5.2 of Chapter 5. Briefly, the locations of animals within exhibits were recorded onto paper maps of the exhibit, and then digitised within a GIS containing spatially-referenced images of the exhibit. This enabled the calculation of the distances between individuals, in metres, which formed the basis of calculations of indices of association for every dyad in the study.

3.5. Assessing animal personality

This research uses a trait rating method to assess the personality of cheetahs held in zoos in the EEP region. Zoos are an excellent resource for studying animal personality; zoo keepers, who are the usual source of data, are familiar with their animals and zoos provide researchers the opportunity to conduct longitudinal investigations into various aspects of personality, including heritability and environmental effects (Watters & Powell, 2012). However there has been no published review of the methodology adopted by zoo animal personality researchers, apart from Tetley and O'Hara (2012), a review based on material presented in this section.

3.5.1. Methods of data collection

Animal personality can be evaluated using two methods: trait rating by knowledgeable informants (e.g. zoo keepers) and coding of the animals' behaviour (Gosling, 2001; Meagher, 2009; Freeman & Gosling, 2010; Highfill *et al*., 2010; Watters & Powell, 2012). Zoo animal personality is most commonly assessed through the use of observer ratings, where people who are familiar with the animals are asked to rate them on various personality traits (Tetley & O'Hara, 2012). This typically involves the use of a questionnaire consisting of a list of adjectives, sometimes accompanied by a definition of each, and raters are asked to score individuals on these adjectives using a scale defined by the researcher (Meagher, 2009, but see Dutton *et al*., 1997).

Coding consists of more conventional observations of behaviour using ethograms, and observations are recorded and analysed in the context of personality traits (Gosling, 2001; Highfill *et al*., 2010). Most studies using this method record the behaviour of animals when presented with novel objects (Rouff *et al*., 2005; Blumstein *et al*., 2006; Powell & Svoke, 2008), or during specific behavioural tests (Uher *et al*., 2008). Behavioural coding is

considered to be more objective than keeper ratings, however observers who are coding the behaviours must still use their own judgement to ascertain whether the behaviours they are observing are those defined in the ethogram (Jones & Gosling, 2005; Meagher, 2009). This is true of all behavioural research, yet the reliability and repeatability of studies in which occurrences of behaviour are recorded are rarely questioned (Jones & Gosling, 2005; Vazire *et al*., 2007; Meagher, 2009; Highfill *et al*., 2010). Furthermore, Vazire and colleagues (Vazire *et al*., 2007) found that trait rating was more reliable than behavioural coding in an assessment of chimpanzee personality, and suggested that behavioural codings can in fact be difficult to measure reliably.

Previous reviews of animal personality research revealed that behavioural coding is the most common method of data collection (Gosling, 2001; Smith & Blumstein, 2008; Freeman & Gosling, 2010). Indeed, Freeman and Gosling (2010) found that 89% of primate personality studies used behavioural coding. However, in a recent review of zoo animal personality research, Tetley and O'Hara (2012) found that 80% of studies used keeper ratings. Thus, it would seem that the choice of method in most zoo animal personality research is in contrast to methodological trends in other animal personality studies. Studies of zoo animal personality often involve several institutions, to enable researchers to compare environmental effects and husbandry factors and to obtain information on a large number of animals. The use of questionnaires eliminates the need for researchers to visit every collection participating in the study, whilst simultaneously increasing sample size and allowing data to be collected on many animals from multiple collections (Carlstead, Mellen *et al*., 1999; Carlstead *et al*., 2000; Kuhar *et al*., 2006; Meagher, 2009). In contrast, behavioural coding is time consuming and often not logistically possible in zoo-based studies, depending on the number of collections taking part, as it requires direct observations of behaviour. This may explain the apparent tendency for zoo researchers to rely on keeper ratings alone.

Powell and Svoke (2008) attempted to devise a method for assessing the personality of giant pandas, using behavioural coding when the pandas were presented with novel objects. To test this method, they compared the results of behavioural coding during novel object tests alongside keeper ratings. Both methods enabled the authors to construct personality profiles for each individual, and those constructed using behavioural coding were qualitatively similar to those constructed using keeper ratings. However, the small sample size of four pandas meant there was insufficient power to detect a personality–behaviour relationship (Powell & Svoke, 2008). Since personality is most strongly expressed when animals are presented with novelty (Réale *et al*., 2007), observing and quantifying animals' reactions to environmental enrichment trials such as these may provide insight into personality (Watters & Meehan, 2007; Powell & Svoke, 2008). This method could be useful for quickly assessing specific personality traits with implications for management and welfare, such as fearfulness, in a few individuals (Watters & Powell, 2012). If these assessments are to be relevant, however, the overall components of personality in the given species must first be identified. This requires a large scale, multi-institutional study, similar to those carried out by King and Figueredo (1997) on chimpanzees and Wielebnowski (1999) on cheetahs, in which ratings provided by experienced keepers would be essential for identifying complex traits that may not be easily distinguishable using behavioural coding alone.

3.5.2. Reliability of ratings

In order for the information provided by a personality study to be useful, the assessment of personality must be both reliable and valid (Gosling, 2001; Gosling & Vazire, 2002; Kuhar *et al*., 2006; Meagher, 2009; Freeman & Gosling, 2010). Raters scoring the animals, or coders observing them, must show agreement in their assessments or observations. This can be confirmed by testing inter-rater (or inter-observer) reliability

(Gosling, 2001; Gosling & Vazire, 2002; Martin & Bateson, 2007; Meagher, 2009). Therefore it is important that as many people as possible provide ratings for each animal, and that those providing the ratings do so independently and do not confer on their answers (Gosling, 2001). Whilst it is not possible to assess inter-rater reliability with only one rater, this should not be considered a barrier to personality research, especially in a multi-zoo study. Tetley and O'Hara (2012) argued animals rated by one person can still be included in overall analyses, and inter-rater reliability calculated for those animals rated by more than one keeper (e.g. Dutton, 2008). Additionally, re-test reliability (Carlstead, Fraser *et al*., 1999) or correlating the ratings with behaviour can indicate the reliability of ratings provided by one person.

Using keeper ratings to assess personality has been criticised for being too subjective, anthropomorphic and not scientific (Gosling & John, 1999; Gosling, 2001; Meagher, 2009; Weiss *et al*., 2012), as it requires keepers to use their judgement to rate the animals based on their own knowledge and impression of the animals and their behaviour (Wemelsfelder, 1997; Gosling, 2001; Highfill *et al*., 2010). However, the increasing body of evidence suggesting that observer ratings are both reliable and valid has added weight to the argument that this method is scientifically credible (Gosling, 2001; Meagher, 2009; Highfill *et al*., 2010). Moreover, there is little evidence supporting the contention that ratings are tainted by anthropomorphism. Kwan *et al*. (2008) found little correlation between self-personality ratings and ratings of dogs (*Canis familiaris*) provided by the same person, suggesting that the raters were not projecting their own characteristics onto their pets. Similarly, Weiss *et al*. (2009) found no cross-cultural differences between ratings of chimpanzee personality obtained from American and Japanese observers, indicating that the cultural backgrounds and experiences of raters do not influence ratings. More recently, Weiss *et al*. (2012) found the same personality dimensions in chimpanzees and orang-utans as had previously been reported, after the interactions between raters and questionnaire items had been removed.

Thus, the preconceptions and expectations of raters could not account for the personality dimensions derived from the ratings (Weiss *et al*., 2012).

Observer ratings have been used to great effect in assessing the welfare and personality of farm animals (Hessing *et al*., 1994) and the personality of companion animals (Feaver *et al*., 1986; Hsu & Serpell, 2003). Indeed, the assessment of personality in domestic dogs has been used to indicate the suitability of individuals for roles as guide dogs (Serpell & Hsu, 2001) and police dogs (Slabbert & Odendaal, 1999), or as family pets (Hennessy *et al*., 2001; Hsu & Serpell, 2003). In the same way, keeper ratings can be used to investigate the welfare and personality of zoo animals.

To ensure that the personality dimensions extracted from trait ratings are as accurate as possible, traits with low inter-rater reliability (i.e. those that keepers are unable to agree on) should be excluded. Inter-rater reliability therefore needs to be examined *a priori* further analysis. Common tests for inter-rater reliability include Kendall's Coefficient of Concordance (e.g. Wielebnowski, Fletchall *et al*., 2002; Martin, 2005; DeCaluwe *et al*., 2013), Spearman's rank-order correlation coefficient (e.g. McKay, 2003; Dutton, 2008; DeCaluwe *et al*., 2013) and intraclass correlations within a General Linear Model, or GLM (e.g. King & Figueredo, 1997; Weiss *et al*., 2007; Uher & Asendorpf, 2008). The most appropriate reliability test will depend on the study design, so it is not possible for researchers to use a single, standard measure of reliability. Furthermore, checking whether reliability tests are significant is often problematic in zoo research, where small sample sizes can mean that the tests are underpowered (Powell & Svoke, 2008) and prone to Type II error. Researchers therefore need to use their own judgement in deciding whether the ratings obtained are reliable or not. For example, Martin (2005) considered raters to be reliable if their ratings correlated with those of another rater.

Research by King and colleagues (King & Figueredo, 1997; Weiss *et al*., 2002, 2006,

2007, 2009; King & Landau, 2003; King *et al*., 2005; Pederson *et al*., 2005) has focused on the reliability and validity of primate personality assessments and the comparison of nonhuman primate personality dimensions with human personality. As well as providing information on the personality of zoo-housed chimpanzees and orang-utans, this body of research has yielded important insights into the methods of assessing personality in zoo animals by using the same questionnaire, developed initially by King and Figueredo (1997), and the same inter-rater reliability tests. The Chimpanzee Personality Questionnaire was first used by King and Figueredo in 1997 to assess the personality of 100 chimpanzees, housed at 12 zoos. The results suggested that chimpanzee personality is composed of five dimensions that are comparable to human personality (the Five Factor Model: Extraversion, Agreeableness, Dependability, Openness and Emotionality) plus one extra dimension: Dominance (King & Figueredo, 1997). Inter-rater reliability was high and there were no significant differences between zoos among the ratings, suggesting that chimpanzee personality remains consistent across different collections (King & Figueredo, 1997). The Chimpanzee Personality Questionnaire has since been developed and applied to other species (Weiss *et al*., 2006, 2009), and is now known as the Hominoid Personality Questionnaire (HPQ).

Powell and Svoke (2008) argued that it may take many months of working with a particular animal before a keeper's ratings are reliable. This issue was briefly addressed by King *et al*., (2005) in their comparative study of the personality of zoo-housed chimpanzees and chimpanzees housed in a naturalistic habitat at an African sanctuary. Zoo keepers had known the animals for an average of 6.5 years, whereas sanctuary staff had a mean of 6.9 months experience with the animals. Inter-rater reliability, assessed by intraclass correlations (King & Figueredo, 1997), showed that the reliability of an individual's ratings was lower among the sanctuary raters (between 0.17 and 0.51) than the zoo raters (between 0.43 and

0.76). However, each sanctuary chimpanzee was rated by a mean of 16.2 raters, so the reliability of mean ratings across all raters was higher (between 0.77 and 0.94). The limited experience of the sanctuary raters was therefore mitigated by the large number of people providing the ratings (King *et al*., 2005).

The experience of raters clearly affects their ability to provide reliable ratings (Dutton *et al*., 1997; King *et al*., 2005; Weiss *et al*., 2007). Researchers should therefore endeavour to obtain information about the experience of those providing ratings and include rater experience as a factor in their analyses (Carlstead *et al*., 2000; Gosling, 2001; Meagher, 2009).

Multi-institutional studies can require keepers from different countries and cultures to provide animal personality ratings, which may affect the reliability of those ratings. Two studies (King *et al*., 2005; Weiss *et al*. 2009) investigated the effects of the language and culture of raters on the reliability of ratings. King *et al*. (2005) translated the HPQ into French to allow the keepers at a French-speaking sanctuary in Africa to rate their animals. This resulted in minor differences in the observed personality structure of the sanctuary chimpanzees, as two factors, Openness and Emotionality, observed in zoo-housed chimpanzees did not replicate in the sanctuary chimpanzees. This discrepancy may have been caused by the small number of adjectives defining the Openness and Emotionality factors (King *et al*., 2005). However, the authors also noted that these differences may have been due to inconsistencies in the translated questionnaire, as no back-translation was carried out to check that the definitions of the adjectives provided in the English version of the questionnaire were the same as those provided in the French version (King *et al*., 2005).

Chimpanzee personality ratings obtained by Weiss *et al*. (2009) in a sanctuary in Japan were compared with those obtained by King and Figueredo (1997) in North America. Unlike the French version of the questionnaire (King *et al*., 2005), the Japanese questionnaire

was back-translated to correct inconsistencies. The ratings obtained by Weiss *et al*. (2009) were as reliable as those obtained by King and Figueredo (1997), and also resulted in six personality dimensions, providing evidence that chimpanzee personality can be reliably assessed by raters of different cultures (Weiss *et al*., 2009). These findings have important implications for future personality assessments in zoos, which must be comparable and consistent when ratings are provided by different cultures of keepers and in different languages.

3.5.3. Validity of ratings

The validity of a personality assessment refers to its ability to accurately measure animal personality (Gosling, 2001; Meagher, 2009). The results must therefore relate to the 'real world' and predict outcomes such as behaviour or breeding success (Gosling & Vazire, 2002; Pederson *et al*., 2005; Uher *et al*., 2008).

Discriminant validity examines the lack of correlation between measures of two traits that are theoretically unrelated (Campbell & Fiske, 1959; Meagher, 2009; Freeman & Gosling, 2010). Few studies described the assessment of discriminant validity, although King and Figueredo (1997), Weiss *et al*. (2002) and King *et al*. (2005) argued that ratings made using the HPQ were theoretically valid because the results demonstrated factor independence, as there were weak correlations between the six personality factors.

Convergent validity examines the relationship between a personality trait and other measures to which it is theoretically similar (Campbell & Fiske, 1959; Meagher, 2009; Freeman & Gosling, 2010). Fearfulness in cheetahs was positively correlated with the amount of time taken to approach a mirror, and cheetahs rated as more aggressive were significantly more likely to growl, hiss and stare at their mirror image (Wielebnowski, 1999). Similarly, fearfulness was positively correlated with the amount of time taken for black rhinoceros to

approach a paper towel (Carlstead, Mellen *et al*., 1999). Convergent validity can also be demonstrated by correlating traits with biological factors, for example adrenal activity (e.g. Wielebnowski, Fletchall *et al*., 2002) or ovarian cyclicity (e.g. Freeman *et al*., 2009), or with quantitative records of behaviours related to the trait (e.g. King & Landau, 2003; Pederson *et al*., 2005). Interestingly, in the study carried out by Powell *et al.* (2008), keeper ratings of socio-sexual behaviour were used to validate personality profiles obtained from behavioural coding during novel object tests, rather than the more conventional method of using ratings to construct personality profiles. This study uncovered a link between shyness and the frequency of socio-sexual behaviour in female pandas, which suggests that the personality profiles were validated by keepers' ratings of behaviour.

Trait ratings can also be validated by carrying out repeat surveys months or years after the initial collection of data. Carlstead, Mellen *et al*. (1999) repeated their initial survey of black rhinoceros after two years. They found significant, positive correlations between the initial keeper ratings and the results of the repeated survey, and the same relationships between personality, behaviour, age and breeding success. Similarly, Uher and Asendorpf (2008) found high stability in keeper ratings of great ape personality, assessed using Crohnbach's alpha and Pearson's correlation coefficient, when the survey was repeated after five weeks. Horback *et al*. (2013) also demonstrated temporal stability of trait ratings of African elephants, with significant correlations between ratings collected one year apart. A repeat survey of cheetah keepers was not possible in the present research due to time constraints. Nonetheless, the repeatability of other surveys of animal personality provides further evidence of the reliability and validity of keeper ratings.

Evidence from the growing body of research into zoo animal personality demonstrates that zoo keepers are able to reliably rate animal personality traits based on their knowledge and long term observations of the animals in their care (King & Figueredo, 1997; Carlstead,

Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999; Wielebnowski, 1999; Wielebnowski, Fletchall *et al*., 2002; Kuhar *et al*., 2006; Whitham & Wielebnowski, 2009; Freeman *et al*., 2010b; Horback *et al*., 2013). Using keeper ratings to assess personality facilitates the collection of data on many individuals at different institutions, and the ratings of zoo keepers working in different zoos, in different countries, speaking different languages can be reliable indicators of animal personality (King & Figueredo, 1997; King *et al*., 2005; Weiss *et al*., 2009).

3.5.4. Methods of assessing felid personality

A summary of previously published research on personality in zoo-housed felids can be found in Table 3.2. To date, eight published studies have investigated felid personality in zoos. All of these studies adopted a trait rating method, and the results showed that keepers are able to reliably rate felid personality traits. Most studies validated trait ratings with observations of behaviour and biological measurements. Wielebnowski (1999) found that cheetahs rated as more aggressive by their keepers were more likely to hiss, growl and stare at their mirror image. Similarly, DeCaluwe *et al*. (2013) observed more hiding behaviour and elevated faecal glucocorticoid metabolite levels in clouded leopards rated as anxious.

The present research is the first of its kind to assess cheetah personality across the EEP region. Since it was not logistically possible to visit every potential participating zoo, a trait rating method was adopted for this research in order to maximise the number of cheetahs for which personality data were obtained. Ratings were received for 120 cheetahs living in 31 zoos; the largest sample of individuals to be rated in any study of felid personality to date (Table 3.2). Detailed procedures for the collection of personality data can be found in Section 6.2 of Chapter 6. In summary, a previously developed questionnaire (Wielebnowski, 1999; Appendix 3) was adapted for this research and the reliability of ratings was examined using

Kendall's coefficient of concordance where three or more keepers provided ratings, and Spearman's rank-order correlation coefficient where two keepers provided ratings (DeCaluwe *et al*., 2013). The questionnaire results were validated by comparing a sub-sample of the ratings with behavioural data; behavioural observations conducted at UK zoos were compared to trait ratings of the same animals.

Table 3.2. Summary of published personality research on zoo-housed felids

Author	Species	Sample size	Focus of study	Assessment of reliability	Assessment of validity
Baker and Pullen (2013)	Cheetah	35	Comparison of personality with housing and husbandry variables	Intra-class correlation coefficient ICC(3, *k*). Traits with mean ICC of < 0.6 removed	Novel object tests
DeCaluwe *et al*. (2013)	Clouded leopard	16	Assessment of adrenal activity and behaviour	Kendall's coefficient of concordance (*W*), from 0.38 to 0.86; Spearman's rank-order correlation coefficient (r_s), from 0.17 to 0.95	Behavioural observations, comparison with faecal corticoid concentration
Gartner and Powell (2012)	Snow leopard	11	Comparison of keeper ratings and behavioural observations	Kendall's coefficient of concordance (*W*), from 0.21 to 0.66; Spearman's rank-order correlation coefficient (r_s), $p<0.05$	Novel object tests
Gartner and Weiss (2013b)	Scottish wildcat	25	Relationship between personality and subjective well-being	Intra-class correlation coefficients ICC(3, 1) from 0.04 to 0.75 and ICC(3, *k*) from 0.10 to 0.89	Not assessed
McKay (2003)	Cheetah	41	Individual breeding success	Spearman's rank-order correlation coefficient (r_s), from 0.72 to 0.98	Novel object tests
Phillips and Peck (2007)	Bengal tiger	7	Keeper/animal interactions	Friedman's test, $p<0.001$ for 13 of 27 adjectives	Behavioural observations
Wielebnowski (1999)	Cheetah	44	Individual breeding success	Kendall's coefficient of concordance (*W*), from 0.57 to 0.98	Novel object tests
Wielebnowski, Fletchall *et al*. (2002)	Clouded leopard	72	Assessment of adrenal activity, behaviour and husbandry	Kendall's coefficient of concordance (*W*). Traits with <80% agreement removed	Comparison with faecal corticoid concentration

3.6. Ethical approval

All research protocols were approved by the University of Salford's Research Ethics Panel. Support for the study was obtained from the British and Irish Association of Zoos and Aquariums (BIAZA) Research Group and permission to conduct behavioural observations was granted by the participating zoos prior to the commencement of data collection.

3.7. Conclusion

This chapter has presented background information on the methods used to collect behavioural data, a discussion of the use of indices of association and GIS in animal behaviour research and a review of data collection methods for assessing zoo animal personality. The following three research chapters provide detailed descriptions of the procedures used for data collection and present the findings of the research.

4. The effects of social group housing on captive cheetah behaviour

4.1. Introduction

4.1.1. Background

Animals living in zoos should, when possible, be kept in naturalistic social groups. Modern animal welfare legislation requires that animals should be kept in such a manner that satisfies their biological requirements (e.g. Art 3 of the Council Directive 1999/22/EC of 29 March 1999 relating to the keeping of wild animals in zoos). This includes the opportunity to exhibit normal behaviour, which incorporates social behaviour. Appropriate social housing is an effective way of improving animal welfare by providing animals the context in which to express wild-counterpart behaviour (De Rouck *et al*., 2005; Price & Stoinski, 2007; Swaisgood & Schulte, 2010). This can also directly affect reproductive success (Mellen, 1991; Carlstead & Shepherdson, 1994; Kleiman, 1994; Lindburg & Fitch-Snyder, 1994; Wielebnowski, 1998), educate zoo visitors about the behaviour of wild animals (Caro, 1993) and optimise the use of available accommodation. In contrast, inappropriate social groupings in captivity can have negative consequences for animal welfare (Morgan & Tromborg, 2007; Price & Stoinski, 2007; Davis *et al*., 2009; Swaisgood & Schulte, 2010).

In the wild, competition for resources (especially food) limits the size of social groups. However in captivity, such resources are plentiful. This allows for flexibility in the types and sizes of social groups that can be maintained, and, coupled with the constraints of finite enclosure space, has led to the housing of naturally solitary species in social groups (Price & Stoinski, 2007; Swaisgood & Schulte, 2010). Some animals benefit from this practice and adapt well to living in a group. Orang-utans, for example, would not normally live in social groups in the wild but are often successfully group-housed in zoos and benefit from social interaction (Perkins, 1992; Price & Stoinski, 2007). Similarly, Shepherdson *et al*. (2013)

found that stereotypic pacing in polar bears decreased as group size increased. However, not all solitary species can be successfully housed with conspecifics.

There is evidence in the literature that solitary felids, in particular, can suffer chronic stress and reduced reproductive success when housed in groups (Mellen, 1991; Jurke *et al*., 1997; Mellen *et al*., 1998; Wielebnowski, Ziegler *et al*., 2002; Swanson *et al*., 2003). Jurke *et al*. (1997) concluded that elevated faecal cortisol levels of socially housed female cheetahs indicated chronic physiological stress, which led to reproductive suppression in some individuals. Similarly, Wielebnowski and colleagues (Wielebnowski, Ziegler *et al*., 2002) found that female cheetahs housed in pairs displayed increased pacing behaviour and aggression, and reduced ovarian activity than did singly housed females. Even individuals that do not display outward behavioural signs of stress, and appear to be compatible, may not reproduce successfully (Kleiman, 1994).

Cheetahs in the wild have a complex social system that is rare among mammals. Adult females are solitary unless accompanied by cubs (Caro, 1994; Wielebnowski, Ziegler *et al*., 2002; Terio *et al*., 2003). Whilst there are conflicting reports of females tolerating one another and congregating around resources (Durant, 1998; Durant *et al*., 2010), as well as actively avoiding one another (Caro, 1994), there is no evidence of adult female cheetahs living together in permanent social groups (Schaller, 1972; Caro, 1994). Males can be solitary, but up to 60% of wild male cheetahs live in small social groups, termed coalitions. Coalitions often consist of littermates, but siblings can be joined by non-relatives to form coalitions of three or four individuals (Caro, 1993, 1994; Durant *et al*., 2004; Gottelli *et al*., 2007). Affiliative interactions are frequent among coalition members and overt aggression is rare, even around kills and in the presence of females (Caro, 1994).

Some authors have suggested that social group housing may be important in determining reproductive success in captive cheetahs (Caro & Collins, 1986; Caro, 1993;

Wielebnowski, Ziegler *et al*., 2002). Long-term studies have been carried out into the social behaviour of wild cheetahs (Caro, 1994), however little is known about the effects of social group housing on captive cheetah behaviour (Ruiz-Miranda *et al*., 1998). The Association of Zoos and Aquariums (AZA) Husbandry Manual for the cheetah states that males can be housed either singly or in coalitions, that male siblings should remain together for life, and that compatible females may be housed in groups (Ziegler-Meeks, 2009). Despite the variation in composition of captive cheetah groups, the potential consequences of inappropriate social housing and the poor reproductive success of the captive population, few published studies have examined in detail the behaviour of captive cheetahs housed in different social groups.

4.1.2. Objective and hypothesis

This chapter aims to address Objective 1 of the research:

- *To compare the behaviour and activity of captive cheetahs housed in natural and unnatural social group types.*

Appropriate social group housing is essential for animal welfare (Morgan & Tromborg, 2007; Price & Stoinski, 2007). It is hypothesised that cheetahs housed in natural social groups (i.e. those group-types that have been observed in wild populations) will display species-specific social behaviours; and those housed in unnatural groups (i.e. those that have not been observed in wild populations) will exhibit increased pacing behaviour, typically associated with stress and reduced welfare (Wielebnowski, Ziegler *et al*., 2002). Further, it is predicted that institutions housing their cheetahs in natural social groups will have better reproductive success than those housing their cheetahs in unnatural social groups (Mellen, 1991).

Objective 1 is investigated using behavioural observations of 37 cheetahs, housed in different social groups at 11 UK zoos. The social behaviour and activity of individuals housed

in groups that occur in the wild; groups that occasionally occur in the wild; and groups that do not occur in the wild were compared. Institutional breeding success was investigated using data from the International Cheetah Studbook, and compared with the types of social groups in which the cheetahs at each zoo were housed.

4.1.3. Outline of the chapter

A review of the literature relevant to this chapter is presented in Chapter 2. Issues relating to the maintenance of social groups in captivity are outlined in Section 2.2, and information on cheetah social organisation is presented in Section 2.6. Background information on the methodological approach is presented in Section 3.2 of Chapter 3, which reviews common methods used in behavioural data collection and presents a justification for the methods adopted in this research.

Section 4.2 of this chapter describes the study sites and subjects selected for behavioural observations. Detailed procedures for the collection and analysis of behavioural data are described in Section 4.3. Section 4.4 presents the results, divided into Sub-section 4.4.1 on the behaviour and activity of cheetahs housed in different groups, Sub-section 4.4.2 on social interactions and Sub-section 4.4.3 on institutional reproductive success. Finally, Section 4.5 discusses the findings of behavioural observations and the implications of these findings for captive cheetah management.

4.2. Study sites and subjects

Eleven UK zoos were selected for data collection visits: Africa Alive!, Suffolk; Banham Zoo, Norfolk; Chester Zoo, Cheshire; Exmoor Zoo, Devon; Marwell Wildlife, Hampshire; Paignton Zoo, Devon; Paradise Wildlife Park, Hertfordshire; Port Lympne, Kent;

West Midland Safari Park, Worcestershire; Wildlife Heritage Foundation, Kent and ZSL Whipsnade Zoo, Bedfordshire. A range of social groups were required for the research, both natural and unnatural, so study sites were selected based on the types of social groups they maintained, as well as the feasibility of travelling to each site for data collection. The selected zoos housed their cheetahs either alone or in groups of between two and five individuals. Groups consisted of related and unrelated males, related and unrelated females, mixed sex adults and one female with cubs (Table 4.1). Twenty-six dyads were represented in the sample: ten dyads were full siblings and 16 dyads were unrelated (Table 4.2).

Table 4.1. Composition of cheetah social groups at eleven UK zoos visited for behavioural observations.

Subject IDs	Group composition	Zoo
Jake, Brooke & Oscar	Related males	ZSL Whipsnade Zoo
Moshi & Sifiso	Related males	Port Lympne
Belika, Munya, Cheetor & Duma	Related and unrelated males	West Midland Safari Park
Burba, Singa & Matrah	Related and unrelated males	Chester Zoo
Maktoum & Al Safa	Unrelated males	ZSL Whipsnade Zoo
Joshi	Single male	Africa Alive!
Kasai	Single male	Paignton
Nescio	Single male	Port Lympne
Quartz	Single male	Africa Alive!
Shaka	Single male	Africa Alive!
Turkus	Single male	Marwell Wildlife
Adaeze	Single female	Chester Zoo
Adjovi	Single female	Banham Zoo
Etna	Female with 3 cubs/single female	Africa Alive!
Tosca	Single female	Paignton Zoo
Izzy & Split	Related females	Port Lympne
Suki & Juba	Related females	Marwell Wildlife
Azizi, Epesi, Kiwara & Zuri	Related and unrelated females	West Midland Safari Park
Dave & Nina	Mixed-sex adults	Exmoor Zoo
Mia, Murphy & Xana	Mixed-sex adults	Paradise Wildlife Park

Table 4.2. Relationships between 26 dyads represented in the sample.

Subject IDs	Relatedness	Sex	Zoo
Belika & Munya	Siblings	Male	West Midland Safari Park
Burba & Singa	Siblings	Male	Chester
Jake & Brooke	Siblings	Male	ZSL Whipsnade Zoo
Jake & Oscar	Siblings	Male	ZSL Whipsnade Zoo
Oscar & Brooke	Siblings	Male	ZSL Whipsnade Zoo
Moshi & Sifiso	Siblings	Male	Port Lympne
Azizi & Epesi	Siblings	Female	West Midland Safari Park
Izzy & Split	Siblings	Female	Port Lympne
Suki & Juba	Siblings	Female	Marwell Wildlife
Dave & Nina	Siblings	Mixed-sex	Exmoor Zoo
Burba & Matrah	Unrelated	Male	Chester
Singa & Matrah	Unrelated	Male	Chester
Belika & Cheetor	Unrelated	Male	West Midland Safari Park
Belika & Duma	Unrelated	Male	West Midland Safari Park
Cheetor & Duma	Unrelated	Male	West Midland Safari Park
Cheetor & Munya	Unrelated	Male	West Midland Safari Park
Duma & Munya	Unrelated	Male	West Midland Safari Park
Maktoum & Al Safa	Unrelated	Male	ZSL Whipsnade Zoo
Azizi & Kiwara	Unrelated	Female	West Midland Safari Park
Azizi & Zuri	Unrelated	Female	West Midland Safari Park
Epesi & Kiwara	Unrelated	Female	West Midland Safari Park
Epesi & Zuri	Unrelated	Female	West Midland Safari Park
Kiwara & Zuri	Unrelated	Female	West Midland Safari Park
Mia & Xana	Unrelated	Female	Paradise Wildlife Park
Mia & Murphy	Unrelated	Mixed-sex	Paradise Wildlife Park
Murphy & Xana	Unrelated	Mixed-sex	Paradise Wildlife Park

A data collection schedule was devised prior to the commencement of field visits (Table 4.3); however it was necessary to revise this schedule due to financial constraints (Table 4.4). Nonetheless, 25 field visits were made between May 2011 and July 2013, and a total of 784 hours of behavioural observations were carried out on 37 cheetahs (22 males and 15 females) at the 11 zoos.

Table 4.3. Planned data collection schedule. Numbers inside cells indicate the planned number of observation days.

Zoo	2011									2012												2013						
	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Africa Alive!		**6**								**6**							**6**											
Banham Zoo		**6**								**6**							**6**											
Chester Zoo	**6**								**6**							**6**												
Exmoor Zoo			**6**								**6**							**6**										
Marwell Wildlife				**6**								**6**							**6**									
Paignton Zoo			**6**								**6**							**6**										
Paradise Wildlife Park	**6**								**6**							**6**												
Port Lympne					**6**								**6**							**6**								
West Midland Safari Park						**6**									**6**						**6**							
Wildlife Heritage Foundation					**6**								**6**							**6**								
ZSL Whipsnade Zoo				**6**								**6**							**6**									

Table 4.4. Schedule of actual data collection visits. Numbers inside cells indicate the number of observation days spent at the study sites.

Zoo	2011									2012												2013							Total hours
	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	
Africa Alive!										**5**																		**6**	61.3
Banham Zoo											**5**																		22.9
Chester Zoo				**6**				**3**	**3**				**6**																102.2
Exmoor Zoo				**6**																									41.3
Marwell Wildlife					**6**								**5**			**5**													108
Paignton Zoo				**6**												**6**													80.8
Paradise Wildlife Park		**6**													**5**														75.8
Port Lympne		**6**												**6**															81.7
West Midland Safari Park				**6**			**2**	**2**				**6**		**2**															96
Wildlife Heritage Foundation														**5**															34
ZSL Whipsnade Zoo					**6**									**6**															80.7

The number of hours of observation collected for this research is large in comparison with other behavioural studies of captive felids. Skibiel *et al*. (2007) studied the effects of different types of enrichment on six species of felids, and collected a total of 238 hours of behavioural data on 14 individuals. Similarly, in their recent study of enrichment methods for captive cheetahs, Quirke and O'Riordan (2011) collected 187.5 hours of behavioural observations of 12 individuals. Mallapur and Chellam (2002) conducted a multi-zoo study on the behaviour and activity of 16 leopards, and carried out 612 hours of behavioural observations. However, each cat was only studied for four days in total, and two were studied off-exhibit only. In their study of the behaviour and hormonal activity of pair-housed female cheetahs, Wielebnowski and her colleagues (Wielebnowski, Ziegler *et al*., 2002) collected 364 hours of behavioural data on eight individuals, and observations were made twice weekly in 30-minute sessions. The present research adopted a rigorous data collection schedule, with repeat visits to study sites and whole days of behavioural observations, to enable data that are representative of actual behavioural patterns to be collected.

At all study sites, water was available *ad libitum* and cheetahs were fed either whole rabbit or chicken carcasses, or portions of beef or horse meat on the bone. However, feeding schedules varied among collections and not all cheetahs were fed on-show. All enclosures were furnished with trees and logs, and contained small, on-show shelters. Decisions concerning which animals had access to on-show enclosures were made by the keeping staff at each study site, and I had no control over which animals were visible on a given day. The animals, enclosures and husbandry routines at each of the eleven study sites are described in the following sub-sections.

4.2.1. Africa Alive!

Visits to Africa Alive! were made in January 2012 for five days and July 2013 for six days. Africa Alive! housed Etna and Joshi during the first visit in January 2012 (Table 4.5). Joshi died in April 2012 and Etna, Quartz and Shaka were housed at Africa Alive! during the repeat visit in July 2013 (Table 4.5). Quartz had previously been observed at Banham Zoo in February, 2012 (Table 4.6).

Table 4.5. Study subjects housed at Africa Alive!

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation		
				January 2012	July 2013	Total
Etna	9	F	Not related	15	17	32
Joshi	13	M	Not related	10.3	-	10.3
Quartz	5	M	Not related	-	12.6	12.6
Shaka	2	M	Not related	-	6.3	6.3

The cheetah exhibit consisted of one large enclosure, two small side enclosures, and one off-show enclosure. During the first visit, Etna was housed with her three, 5-month old cubs, separately from Joshi, who was housed alone. Either Etna and her cubs or Joshi were given access to the large enclosure on alternate days. Data were collected on only Joshi and Etna, because Etna's cubs could not easily be distinguished from one another. During the second visit, Etna, Quartz and Shaka were housed separately and one individual was given access to the large enclosure each day. Behavioural observations were conducted only on the individuals occupying the large enclosure, as the side enclosures could not be easily viewed.

The cheetahs at Africa Alive! were fed on-exhibit at the end of the day, with two starve days per week. Etna was fed every day when she had cubs. The cheetah in the large enclosure received an additional small piece of food during daily educational talks in the afternoons.

4.2.2. Banham Zoo

One 5-day visit was made to Banham Zoo, which housed Adjovi and Quartz (Table 4.6), in February 2012. The cheetah exhibit consisted of one large outdoor enclosure and two indoor, off-show dens. Adjovi and Quartz were housed separately and often only one individual had access to the outdoor, on-show enclosure at a time, whilst the other remained indoors, off-show. For most of the visit Adjovi was given access to the outdoor enclosure during the day and Quartz was housed indoors. However, Adjovi and Quartz were being gradually introduced to one another for breeding at the time of the visit, and shared the outdoor enclosure for up to two hours per day (a total of 9.3 hours of observation). Since the behaviour of both Quartz and Adjovi was affected by the presence of the other, it was decided to remove the hours during which they shared the outdoor enclosure from the analysis. This resulted in a total of 12 hours of observation of Adjovi and only 1.6 hours of observation of Quartz. Given that Quartz was also observed at Africa Alive! (Table 4.5), the 1.6 hours during which he was observed at Banham Zoo were excluded from further analysis. The cheetahs at Banham Zoo were fed on-exhibit at the end of the day and the cheetah in the large enclosure received an additional small piece of food during daily educational talks in the afternoons.

Table 4.6. Study subjects housed at Banham Zoo.

Subject ID	Age at time of observation (years)	Sex	Relationship	Hours of observation
Adjovi	8	F	Not related	12
Quartz	3	M	Not related	1.6

Funds became available for a repeat visit to Banham Zoo in July 2013. However, it was decided that a repeat visit would not be made because Adjovi died in June 2012, Quartz had been moved to Africa Alive! and Etna's cubs had been moved to Banham Zoo. Thus, a

repeat visit to Banham would not have yielded more hours of observation of either Adjovi or Quartz.

4.2.3. Chester Zoo

Chester Zoo housed five adult cheetahs, four of whom were visible for behavioural observations during three data collection visits (Table 4.7). The outdoor exhibit consisted of two large enclosures measuring 1975m^2 and 690m^2 and four smaller enclosures measuring 497m^2, 288m^2, 225m^2 and 238m^2. The large enclosures and two of the four small enclosures were easily viewable from the visitor areas. In July, November and December 2011, only the three males, Burba, Singa and Matrah, were on-show, and had access to various combinations of the 690m^2, 497m^2 and 288m^2 enclosures. Siblings Burba and Singa had been housed together since birth and had been introduced to Matrah in 2008 (Chadwick *et al*., 2013). Adaeze was on-show in the 1975m^2 enclosure in April 2012, but was periodically housed off-show whilst the keepers carried out enclosure maintenance. Additional data were collected on the group of males during these times, as they remained on-show. A second female, Kinky Tail, was housed off-show with her newborn cubs in July 2011, then in the 238m^2 enclosure during subsequent visits. No observations were carried out on Kinky Tail and her cubs as they were not easily viewable from the visitor areas.

Table 4.7. Study subjects housed at Chester Zoo.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation			
				July 2011	Nov/Dec 2011	April 2012	Total
Enclosure 1							
Burba	4	M	Full sibling	42	29.5	9.2	80.7
Singa	4	M	Full sibling	42	29.5	9.2	80.7
Matrah	4	M	Not related	42	29.5	9.2	80.7
Enclosure 2							
Adaeze	5	F	Not related	-	-	21.5	21.5

The cheetahs at Chester Zoo were fed once daily, on exhibit. The keepers arrived in the afternoons to feed the cheetahs and clean the enclosures. The keepers at Chester did not enter the enclosure with the cheetahs, so the three males were restricted to one of the 690m^2, 497m^2 and 288m^2 enclosures and Adaeze was temporarily housed off show whilst the keepers carried out their cleaning duties.

4.2.4. Exmoor Zoo

Siblings Dave and Nina were housed together at Exmoor Zoo (Table 4.8). At the request of the EEP, neither of these individuals were recommended for breeding. This site was included in the study because Dave and Nina were housed in an unnatural-type group; groups of mixed-sex adults have not been observed in the wild. One 6-day visit was made to Exmoor in July 2011. The cheetahs were fed daily in the morning, before the zoo opened, and received an additional small piece of food at 1330h during a public talk given by one of the keepers. No repeat visits were made to Exmoor because Nina died in January 2013, before the planned returned visit could take place.

Table 4.8. Study subjects housed at Exmoor Zoo.

Subject ID	Age at time of observation (years)	Sex	Relationship	Hours of observation
Dave	8	M	Full sibling	41.3
Nina	8	F	Full sibling	41.3

4.2.5. Marwell Wildlife

Siblings Suki and Juba, and an unrelated male, Turkus, were housed at Marwell Wildlife (Table 4.9). Suki and Juba had been housed together at Marwell since birth. Turkus

had been housed with Suki and Juba since his arrival in 2007, but was separated from the females in June 2011, two months before the first data collection visit. The cheetahs at Marwell were fed once daily, either in the morning before the zoo opened or in the evening, during the last hour before the zoo closed.

Table 4.9. Study subjects housed at Marwell Wildlife.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation			
				August 2011	April 2012	July 2012	Total
Enclosure 1							
Suki	6	F	Full sibling	21	19	14	54
Juba	6	F	Full sibling	21	19	14	54
Enclosure 2							
Turkus	6	M	Not related	21	14	19	54

4.2.6. Paignton Zoo

Visits to Paignton Zoo were made in July 2011 and July 2012 (Table 4.10). The cheetah exhibit consisted of one on-show enclosure and three off-show enclosures. The adult female, Tosca, was on show in July 2011 and the adult male, Kasai, was housed off-show. Kasai occupied the on-show enclosure in July 2012, with Tosca housed off-show. The cheetahs were fed on-exhibit, either in the morning or the evening, and were temporarily housed off-show whilst the keepers carried out routine cleaning and enclosure maintenance once per day.

Table 4.10. Study subjects housed at Paignton Zoo.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation		
				July 2011	July 2012	Total
Tosca	9	F	Not related	42	-	42
Kasai	13	M	Not related	-	38.8	38.8

4.2.7. Paradise Wildlife Park

Visits to Paradise Wildlife Park were made in May 2011 and June 2012. The cheetah exhibit consisted of one outdoor enclosure and three indoor dens, which could also be viewed by the public. Murphy, Mia and Xana (Table 4.11) were housed together in May 2011. Murphy had arrived from Wildlife Heritage Foundation one week before observations began. Mia and Xana had been housed together since Mia's arrival in 2010 and remained together until Xana's death in January 2012. Mia was housed alone in June 2012, as Murphy had returned to Wildlife Heritage Foundation.

The keepers at Paradise Wildlife Park entered the enclosure daily to carry out routine enclosure cleaning and maintenance. The cheetahs were fed once daily, in the evenings. During the second visit, the keepers also entered the enclosure to hand feed Mia during daily public talks and were sometimes accompanied by members of the public as part of a 'Keeper for a Day' experience.

Table 4.11. Study subjects housed at Paradise Wildlife Park.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation		
				May 2011	June 2012	Total
Murphy	3	M	Not related	41	-	41
Mia	2	F	Not related	41	34.8	75.8
Xana	13	F	Not related	41	-	41

4.2.8. Port Lympne

Visits to Port Lympne were made in May 2011 and May 2012. In May 2011, adult male Nescio was housed alone (Enclosure 1, Table 4.12). The enclosure was situated in an area of the park that was not accessible to visitors on foot. Instead, visitors were driven past the enclosure in large safari vehicles on a road that ran along the front of the enclosure. In

May 2012, Nescio had been moved to another collection and male siblings Moshi and Sifiso were housed in this enclosure. Female siblings Izzy and Split were housed in a second enclosure in a different area of the park (Table 4.12). Unlike the enclosure housing the males, the enclosure housing the females was accessible to visitors on foot. The cheetahs at Port Lympne were fed once daily, on-exhibit.

Table 4.12. Study subjects housed at Port Lympne.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation		
				May 2011	May 2012	Total
Enclosure 1						
Nescio	11	M	Not related	41.7	-	41.7
Moshi	2	M	Full sibling	-	20	20
Sifiso	2	M	Full sibling	-	20	20
Enclosure 2						
Izzy	3	F	Full sibling	-	20	20
Split	3	F	Full sibling	-	20	20

A final visit to Port Lympne was planned for July 2013. However, the keepers had begun to introduce the males and females to one another for breeding, and suspected that one of the females was pregnant. Thus, it was decided that a repeat visit to Port Lympne would not be made because the housing arrangements of the cheetahs had changed.

4.2.9. West Midland Safari Park

West Midland Safari Park (WMSP) housed eight cheetahs; four males and four females (Table 4.13). All eight had been housed together in a large enclosure measuring 5679m^2 since their arrival at the park in 2008. In 2010, the enclosure was divided into two smaller areas (measuring 2926m^2 and 2753m^2) and the group was split into one all-male group and one all-female group. The off-show house contained separate dens and was not accessible to the animals during the day. The cheetah enclosure was situated on a safari route

and was a drive-by, rather than a drive-through exhibit. Visitors could view the cheetahs from their vehicles and were not permitted on foot, so behavioural observations at this site had to be made from a vehicle.

In June 2011, the females were housed in the 2926m^2 enclosure and the males were housed in the 2753m^2 enclosure, furthest from the house. Kiwara and Zuri were taken off-show for one day in June 2011, when Kiwara was separated from the other females for veterinary treatment and Zuri was housed with her for companionship. During subsequent visits, the males were housed in the 2753m^2 enclosure and the females were housed in the 2926m^2 enclosure.

The cheetahs at WMSP were brought into the off-show house in the evenings, where they were fed and then remained until the following day. Animals housed in the 2753m^2 enclosure had to pass through the 2926m^2 enclosure to reach the house in the evenings.

Table 4.13. Study subjects housed at West Midland Safari Park.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation				
				June 2011	Oct/ Nov 2011	March 2012	May 2012	Total
Enclosure 1								
Munya	6	M	Full sibling	17.83	9.67	15	4.65	47.15
Belika	6	M	Full sibling	17.83	9.67	15	4.65	47.15
Cheetor	4	M	Not related	17.83	9.67	15	4.65	47.15
Duma	4	M	Not related	17.83	9.67	15	4.65	47.15
Enclosure 2								
Kiwara	4	F	Not related	11	11.33	14.67	5	42
Zuri	4	F	Not related	11	11.33	14.67	5	42
Epesi	4	F	Full sibling	17.67	11.33	14.67	5	48.67
Azizi	4	F	Full sibling	17.67	11.33	14.67	5	48.67

4.2.10. Wildlife Heritage Foundation

One visit was made to Wildlife Heritage Foundation in May 2012. Murphy, who had previously been observed at Paradise Wildlife Park (Table 4.11), was housed alone and observed for 34 hours. Wildlife Heritage Foundation was not open daily to the public, but could be visited by special arrangement and hosted photography sessions and 'Big Cat Encounters'. Small groups of up to fifteen photographers visited the cheetah enclosure in the afternoons, accompanied by a member of staff. Murphy was fed once daily in the evening and temporarily isolated in a small on-show pen whilst the keepers carried out routine cleaning and enclosure maintenance.

4.2.11. ZSL Whipsnade Zoo

ZSL Whipsnade Zoo was visited in August 2011 and May 2012. The cheetah exhibit consisted of two on-show enclosures, measuring 1693m^2 and 2269m^2, and an extensive off-show facility. Unrelated males Maktoum and Al Safa had been housed together since 2008. They occupied the 1693m^2 enclosure and were observed during the first visit (Table 4.14). Siblings Jake, Brooke and Oscar were born at Whipsnade and were housed in the 2269m^2 enclosure in May 2012 (Table 4.14). Whipsnade also housed three other adult cheetahs, one male and two females, in the off-show facility. They were each housed in a separate off-show enclosure and remained off-show during both visits.

The cheetahs at Whipsnade were fed once daily, on-exhibit in the evenings. Access to the off-show dens was only available to the animals overnight and during bad weather. The keepers reported that they occasionally entered the enclosures to carry out their cleaning duties, but this did not happen during behavioural observations.

Table 4.14. Study subjects housed at ZSL Whipsnade Zoo.

Subject ID	Age at time of first observation (years)	Sex	Relationship	Hours of observation		
				August 2011	May 2012	Total
Enclosure 1						
Maktoum	5	M	Not related	46	-	46
Al Safa	5	M	Not related	46	-	46
Enclosure 2						
Jake	2	M	Full sibling	-	34.67	34.67
Brooke	2	M	Full sibling		34.67	34.67
Oscar	2	M	Full sibling	-	34.67	34.67

4.3. Procedures

4.3.1. Behavioural observations

An ethogram was developed during observations of cheetah behaviour prior to the commencement of field visits (Table 4.15; Chadwick *et al*., 2013). Definitions of behaviours were taken from Caro's (1994) study of wild cheetahs in the Serengeti, Wielebnowski's (1999) study of individual differences in the behaviour of captive cheetahs and a study by Skibiel *et al*. (2007) on enrichment types for six species of captive felids: cheetah, cougar (*Puma concolor*), jaguar (*Panthera onca*), lion, ocelot and tiger (*Panthera tigris*).

Table 4.15. Cheetah behaviour ethogram.

Behaviour	**Definition**
Active	
Aggression[2, 3]	Growling, hissing, slapping or biting directed at another.
Climbing[3]	Use of raised items in the enclosure, e.g. logs.
Feeding[3]	Eating, drinking, chewing, or licking edible substances.
Locomotion[2, 3]	Walking, running.
Pacing	Walking repeatedly along a definite path (e.g. along the fence of the exhibit).
Playing alone[2,3]	Engaging in playful activities (seemingly meaningless, but non-aggressive behaviour) alone.
Scent marking[3]	Animal releases spray from posterior toward an object.
Sniffing	Crouching on forelegs with back legs supporting the body, inhaling through the nose.
Social play[2]	Engaging in playful activities (seemingly meaningless, but non-aggressive behaviour) with another.

[1]Caro (1994); [2]Wielebnowski (1999); [3]Skibiel *et al*. (2007).

Table 4.15. cont.

Behaviour	Definition
Active	
Standing[1]	Flank and hindquarters off the ground, forelegs and back legs supporting the body.
Standing alert[1]	Flank and hindquarters off the ground, forelegs and back legs supporting the body. Vigilant: head raised, eyes open and looking around.
Urinating/defecating[3]	Any projection of bodily fluids (except scent marking). Includes vomiting.
Vocalisation[3]	Auditory sound emitted by the mouth.
Inactive	
Allogrooming[1, 2, 3]	Animal licking the fur of another.
Grooming[3]	Animal licking or scratching itself.
Lying alert[1]	Lying with flank and hindquarters on the ground and forelegs tucked under the body. Vigilant: head raised, eyes open and looking around.
Lying flat out[1]	Lying prone with head on the ground.
Lying out[1]	Lying prone with head raised. Occasional rolling over included.
Sitting[1]	Sitting on back legs with forelegs vertically supporting the body.
Sitting alert[1]	Sitting on back legs with forelegs vertically supporting the body. Vigilant: head raised, eyes open and looking around.
Not visible	
In house	Animal is in indoor quarters and its behaviour is not observable
Out of sight	Animal is in outdoor enclosure but its behaviour is not observable.

[1]Caro (1994); [2]Wielebnowski (1999); [3]Skibiel *et al*. (2007).

During the first data collection visit to every zoo, photographs of each cheetah were taken and keeper descriptions were used to identify individuals. Individuals were identified by differences in their facial markings and the banding patterns on their tails (e.g. Figure 4.1). Photographic records have been extensively used for identification in studies of wild cheetahs (Eaton, 1970; Caro & Durant, 1991; Laurenson *et al*., 1992; Caro, 1994) and tail bands have been quantitatively shown to differ between individuals (Caro & Durant, 1991). The correct identification of group housed individuals was especially important for this research, in order to facilitate the detailed investigation of social relationships between related and unrelated individuals.

(a)

(b)

(c)

(d)

Figure 4.1. Photographs used to aid the identification of Cheetor, (a) and (b), and Duma, (c) and (d), at West Midland Safari Park. Note the differences in facial markings and tail bands between the two individuals. Photographs by Kirk Tudor.

Behavioural observations were conducted all day from the public viewing areas, during zoo opening hours. Observation days were between four and seven hours in length, since zoo opening hours varied between sites and according to the season, with longer opening hours during the months of July and August and shorter opening hours during the winter months. Behavioural observations were made between 1000h and 1800h in the summer and 1000h and 1600h in the winter. Where a study site housed more than one group of cheetahs in separate enclosures, observation time was split equally between the enclosures

where possible, and groups were studied on alternate, whole days. Scan sampling and instantaneous recording were used to collect behavioural data (Chapter 3; Altmann, 1974; Martin & Bateson, 2007). All animals in the enclosure were observed throughout the day and behaviour was recorded once per minute (Wielebnowski, Ziegler *et al*., 2002) onto check sheets (Appendix 1). This resulted in an estimate of the time spent by each individual performing each behaviour (Altmann, 1974; Martin & Bateson, 2007). All occurrences of scent marking and grooming were recorded, as well as social behaviours (aggression, allogrooming and social play, Table 4.15) among group-housed cheetahs, whether they occurred on or between sample points (Altmann, 1974; Margulis & Westhus, 2008).

There is the potential for the behaviour of zoo animals to be affected by the presence of visitors around their enclosure (Hosey, 2000; Davey, 2007); thus, the number of visitors present in the public viewing areas was counted once per minute, after the behaviour of the animals had been recorded. At WMSP, the number of visitors' vehicles at the exhibit was counted. Met Office temperature measurements from the nearest weather station were accessed in the field using a smart phone and recorded once every 20 minutes, in order to investigate the effect of temperature on the behaviour and activity of the cheetahs.

4.3.2. Institutional breeding success

Institutional breeding success was compared with the types of social groups in which the cheetahs at each zoo were housed. The International Cheetah Studbook (Marker, 2010, 2011, 2012a, 2012c) was examined to calculate institutional breeding success, defined as the number of litters born (surviving or not) divided by the sum of the years since 2008 that animals over the age of 2 were housed at the zoo (Carlstead, Fraser *et al*., 1999). Studbook data were only available until 2011, and studbooks preceding 2008 were not included in the

calculation because the types of social groups maintained by the zoos prior to 2008 were not known.

Africa Alive! and Banham Zoo frequently exchanged males and females for breeding, so they were treated as one institution and the total number of litters born at both zoos was used for analysis. A similar arrangement was in place between Paradise Wildlife Park and Wildlife Heritage Foundation, so they were also treated as one institution. Exmoor Zoo was not included in the analysis because it did not house breeding animals between 2008 and 2011. Similarly, Port Lympne was also excluded because it did not house cheetahs of both sexes between 2008 and 2011.

4.3.3. Data analysis

To control for the variable amount of time individuals were observed, data were summarised as the percentage of visible scans on which each animal performed each defined behaviour (Stoinski, Kuhar *et al*., 2004). Percentage of visible scans was calculated by dividing the total number of scans an animal was observed performing each behaviour by the total number of scans the animal was visible. Rates of social interactions per visible hour within dyads (aggression and allogrooming, Table 4.15) were calculated by dividing the number of occurrences of each interaction by the number of hours both members of the dyad were visible.

Before testing for differences in the behaviour of cheetahs housed in different social groups, differences in activity and pacing based on age, temperature and gender were analysed using Spearman's rank-order correlation coefficient (age, temperature and visitor numbers) and Mann-Whitney U tests (gender). The effects of temperature on activity were investigated by comparing mean daily temperatures with the daily percentage of visible scans on which active and inactive behaviours were observed in each individual. The effects of

visitor numbers on activity and pacing behaviour were examined by comparing the maximum daily numbers of visitors present in the public viewing areas with the daily percentage of visible scans on which active, inactive and pacing behaviours were observed in each individual. A separate analysis was conducted for the cheetahs at WMSP, with the maximum daily number of visitors' vehicles replacing the number of visitors. Cheetahs housed in Enclosure 1 at Port Lympne (three individuals, Table 4.12) were excluded from the analysis of the effects of visitor numbers, since visitors did not have access to this enclosure.

To investigate the effects of social group housing on behaviour, individuals were grouped according to their housing condition into one of the following categories: social situations that occur in the wild (two or more adult males, singly-housed adult females, females with cubs; n = 18), social situations that occasionally occur in the wild (singly-housed adult males; n = 6) and social situations that do not occur in the wild (two or more adult females, mixed-sex adults; n = 13). Kruskal-Wallis one-way analysis of variance was used to examine differences in activity and pacing behaviour based on social group type. Differences in the rates of allogrooming and aggression within dyads based on dyad type (natural: male-only dyads; unnatural: female-only dyads, mixed-sex dyads) and relatedness were analysed using Mann-Whitney U tests.

Due to the small number of zoos included in the analysis of institutional breeding success, zoos were grouped into two categories: those housing their cheetahs in social groups that do not occur in the wild (two or more adult females, mixed-sex adults; n = 3) and those housing their cheetahs in all other social group types that have been observed in wild populations (two or more adult males, singly housed adult females, singly housed adult males; n = 4). If any of the groups it maintained had not been observed in wild populations, the zoo was placed into the former category for analysis.

4.4. Results

4.4.1. Activity and pacing behaviour

The cheetahs showed more inactive behaviours than active behaviours (inactive: $\overline{x}$ = 57.6% visible scans; active: $\overline{x}$ = 34.1% visible scans). No significant correlation was found between a cheetah's age and the percentage of visible scans he or she spent active (Spearman's rank-order correlation coefficient, r_s = 0.107, n = 37, p>0.05) or pacing (r_s = 0.161, n = 37, p>0.05). There were also no significant differences in the activity and pacing behaviour of males and females (activity: Mann-Whitney, U = 186.0, n_1 = 22, n_2 = 15, p> 0.05; pacing: U = 191.5, n_1 = 22, n_2 = 15, p>0.05). The cheetahs were more active in cold weather than in warm weather, and more inactive in warm weather than cold weather. A significant, negative correlation was found between activity and temperature (Figure 4.2; r_s = -0.563, n = 263, p<0.001) and inactivity was significantly positively correlated with temperature (Figure 4.3; r_s = 0.563, n = 263, p<0.001).

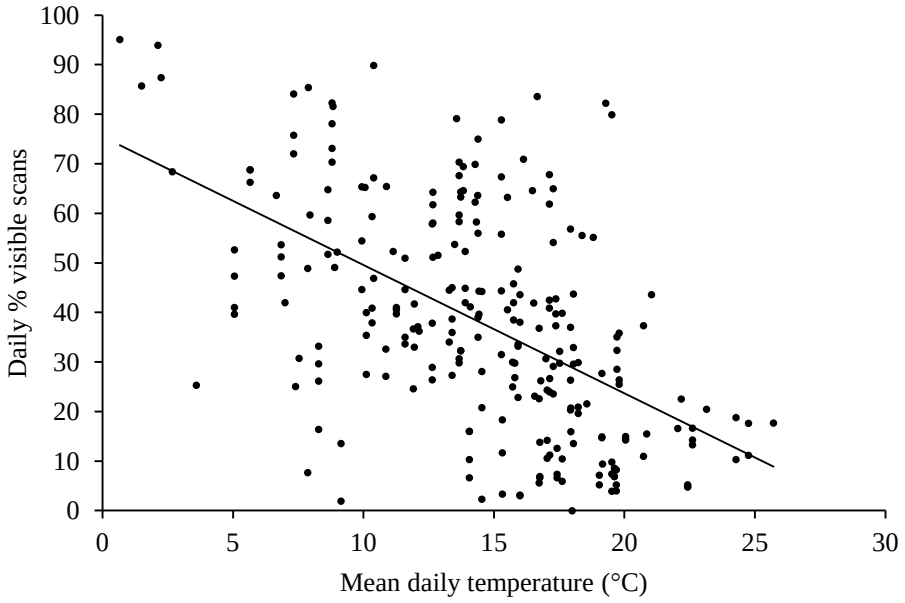

Figure 4.2. The effect of temperature on the mean daily percentage of visible scans on which active behaviours were observed.

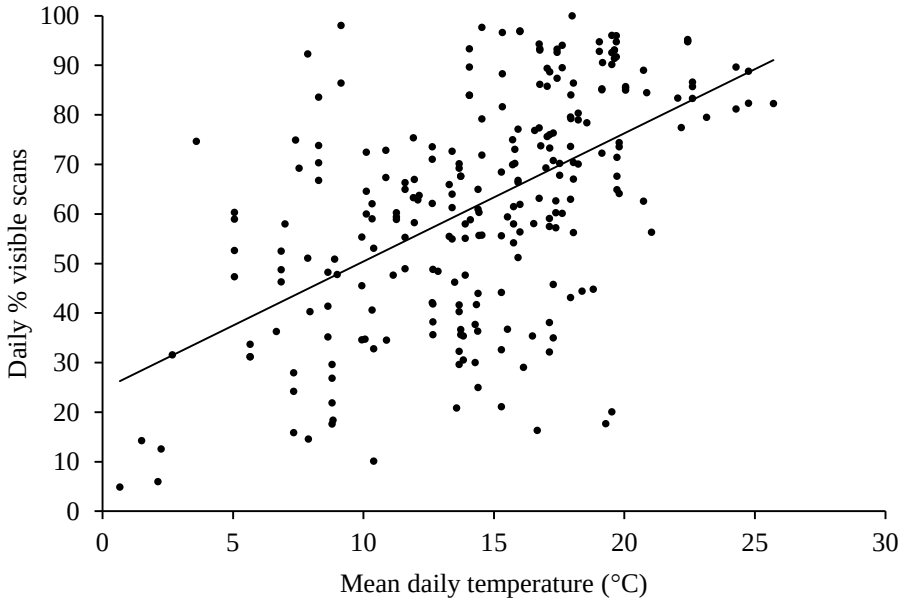

Figure 4.3. The effect of temperature on the mean daily percentage of visible scans on which inactive behaviours were observed.

No significant relationship was found between the maximum daily number of visitors present in the public viewing areas and the daily percentage of visible scans on which pacing behaviour was observed (r_s = -0.073, n = 174, p>0.05). A significant, negative correlation was found between the maximum daily number of visitors and the percentage of visible scans on which active behaviour was observed (r_s = -0.326, n = 174, p<0.001), and a significant, positive correlation was found between the maximum daily number of visitors and the percentage of visible scans on which inactive behaviour was observed (r_s = 0.326, n = 174, p<0.001). However there was also a significant, positive correlation between temperature and visitor numbers (r_s = 0.486, n = 174, p<0.001). Thus, it was decided to carry out partial correlations between activity, inactivity and visitor numbers, controlling for mean daily temperature. When the effects of temperature were controlled for, there were no significant relationships between activity and visitor numbers (active: $r(171)$ = -0.108, p>0.05; inactive: $r(171)$ = 0.108, p>0.05).

At WMSP, no significant relationships were found between the maximum daily number of visitors' vehicles at the exhibit and the daily percentage on which active, inactive or pacing behaviours were observed (active: r_s = -0.054, n = 77, p>0.05; inactive: r_s = 0.054, n = 77, p>0.05; pacing: r_s = 0.087, n = 77, p>0.05).

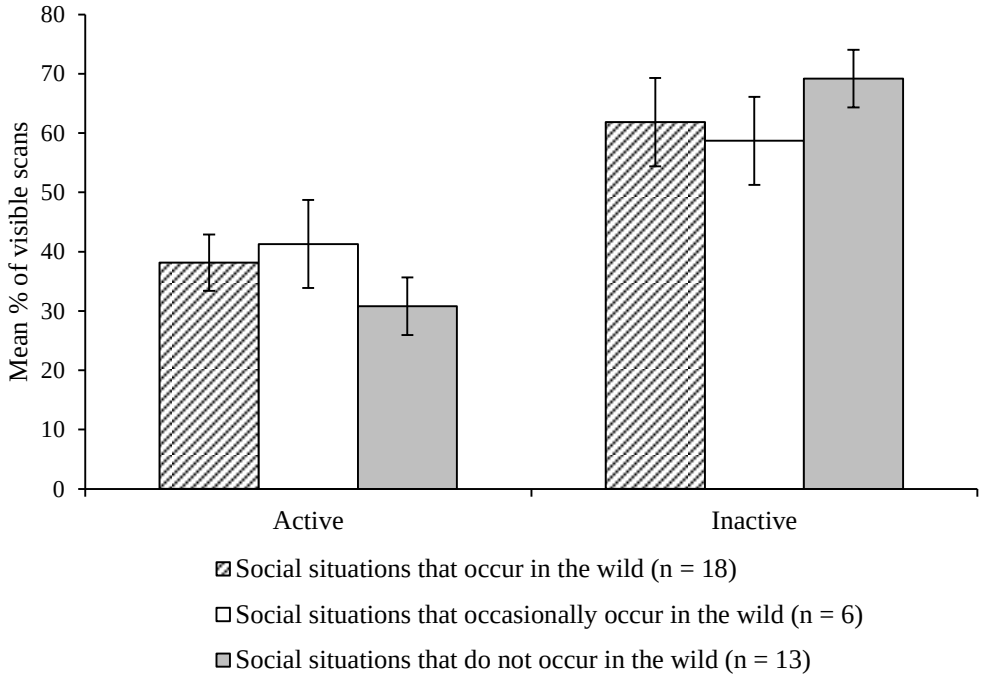

Figure 4.4. Mean percentage of visible scans on which active and inactive behaviours were observed for individuals in the three housing categories. Error bars represent the standard error of the mean.

Individuals housed in groups that occur in the wild showed more active behaviours (Figure 4.4), however there were no significant differences in activity between the three group types (Kruskal-Wallis, H_2 = 1.22, p>0.05). Pacing behaviour, defined as repeatedly walking the same path, was included in the active category of behaviours (Table 4.15). The mean percentage of visible scans on which pacing behaviour was observed was 7.29% (± 1.67%). Individuals housed in social groups that occur in the wild appeared to pace less frequently

than individuals in the other two housing categories, however pacing behaviour did not differ significantly as a function of housing condition (Figure 4.5; $H_2 = 0.99$, $p>0.05$).

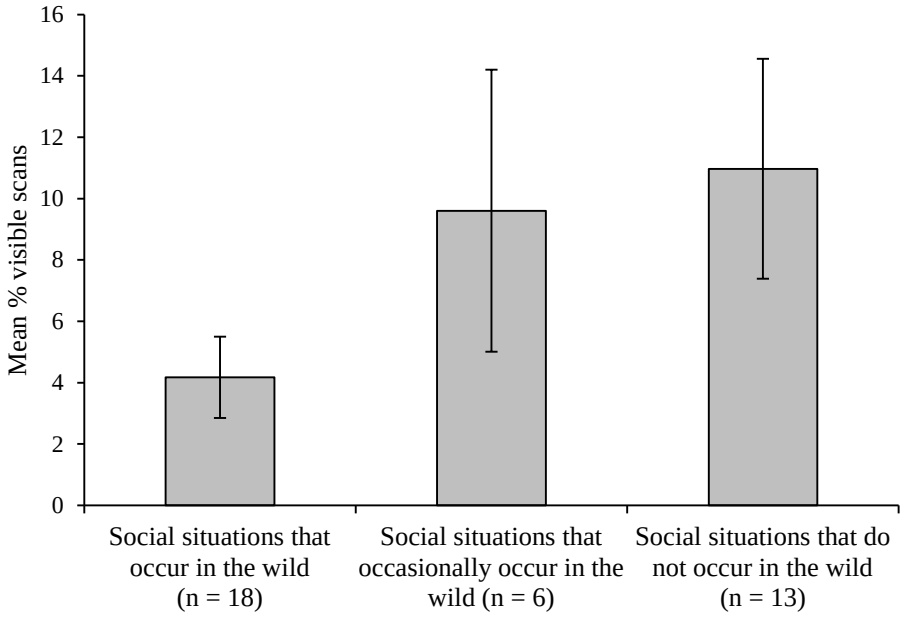

Figure 4.5. Mean percentage of visible scans on which pacing behaviour was observed for individuals in the three housing categories. Error bars represent the standard error of the mean.

4.4.2. Social interactions

Among group-housed individuals, the mean rate of allogrooming was higher than the mean rate of aggression (allogrooming: $\overline{x}$ = 0.67 ± 0.1 occurrences/hr, range 0 to 2.15 occurrences/hr; aggression: $\overline{x}$ = 0.19 ± 0.05 occurrences/hr, range 0 to 0.84 occurrences/hr). No significant differences were found in the rates of allogrooming or aggression within natural and unnatural dyads (allogrooming: Mann-Whitney, U = 69.0, n_1 = 14, n_2 = 12, $p>0.05$; aggression: U = 68.5, n_1 = 14, n_2 = 12, $p>0.05$). The mean rate of allogrooming was significantly higher within related dyads than unrelated dyads (Figure 4.6; U = 35.0, n_1 = 10, n_2 = 16, $p<0.05$). The mean rate of aggression was higher within unrelated dyads than related

dyads; this difference approached significance at the 5% level (U = 117.0, n_1 = 10, n_2 = 16, p = 0.053). During behavioural observations, it was noted that aggressive interactions were more frequent at feeding times. However, not all groups were fed on-exhibit. Thus, in order to compare rates of aggression across all dyads, it was decided to remove those instances of aggression that occurred at feeding times from the data set. When aggression at feeding time was discounted, there was no significant difference in the rate of aggression within natural and unnatural dyads (U = 61.0, n_1 = 14, n_2 = 12, p>0.05). However, the mean rate of aggression was significantly higher within unrelated dyads than within related dyads (Figure 4.6; U = 149.0, n_1 = 10, n_2 = 16, p<0.001).

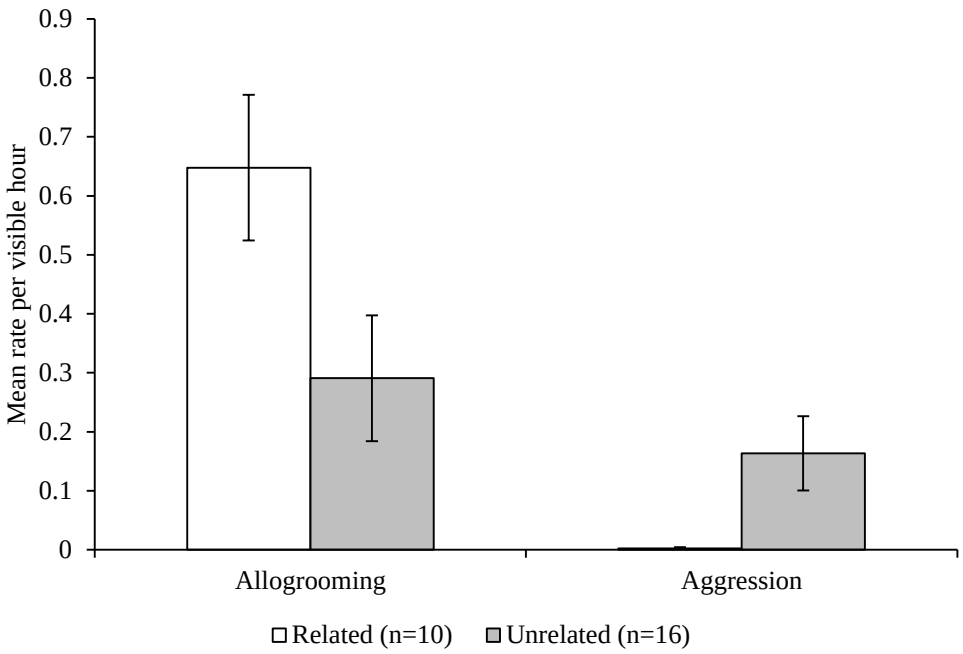

Figure 4.6. Rates of allogrooming and aggression between related and unrelated individuals. Instances of aggression occurring at feeding time were removed from the data set. Error bars represent the standard error of the mean.

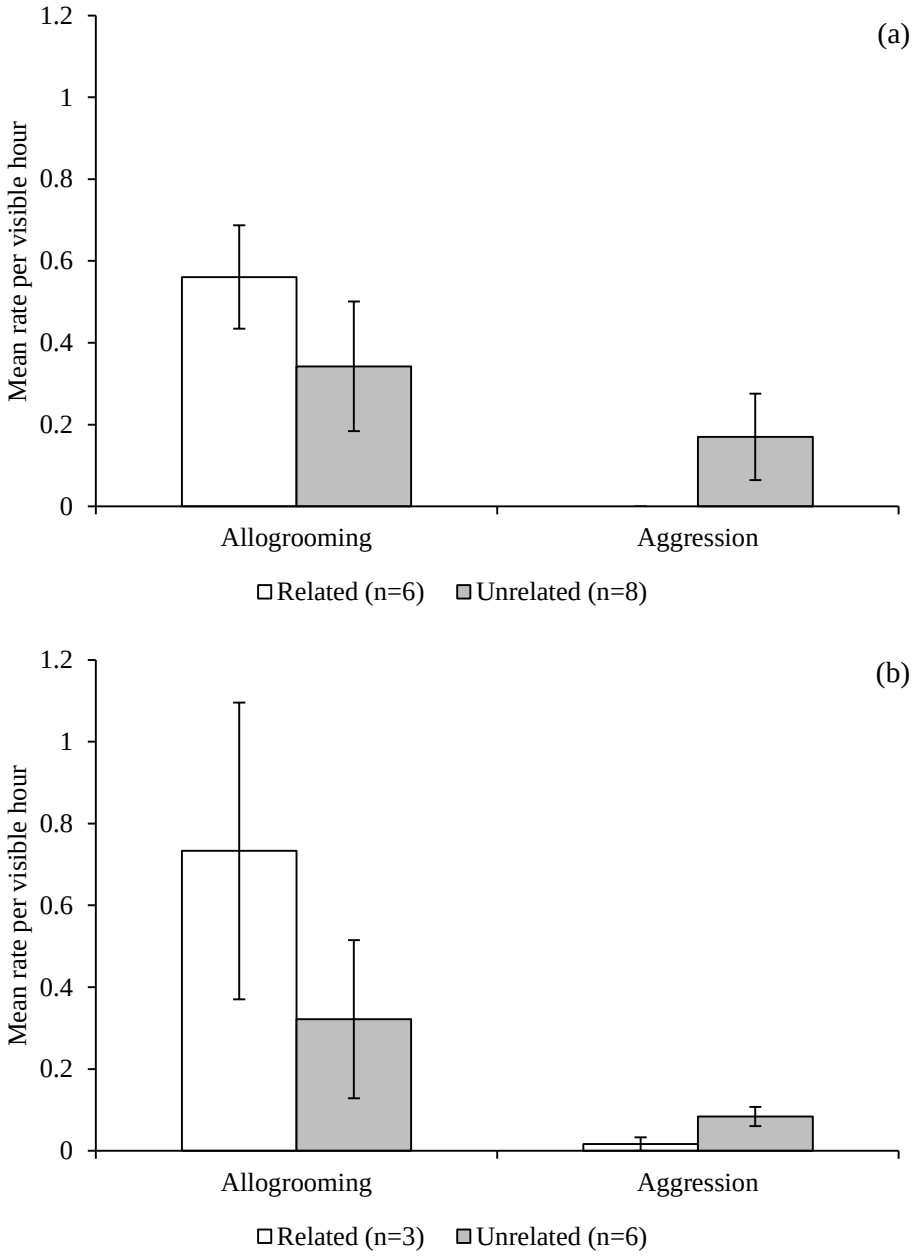

Figure 4.7. Rates of allogrooming and aggression between (a) related and unrelated males and (b) related and unrelated females. Instances of aggression occurring at feeding time were removed from the data set. Error bars represent the standard error of the mean.

The same trends were apparent when interactions within male-only dyads and female-only dyads were examined separately (Figure 4.7). Although not statistically significant, the mean rates of allogrooming were higher between related males than unrelated males, and between related females than unrelated females (males: $U = 13.0$, $n_1 = 6$, $n_2 = 8$, $p>0.05$;

females: $U = 4.0$, $n_1 = 3$, $n_2 = 6$, $p>0.05$). When aggression at feeding time was discounted, unrelated males engaged in significantly more aggressive interactions than related males ($U = 42.0$, $n_1 = 6$, $n_2 = 8$, $p<0.05$). Among related males, aggression was only observed at feeding times. Unrelated females also engaged in significantly more aggressive interactions than related females ($U = 18.0$, $n_1 = 3$, $n_2 = 6$, $p<0.05$).

4.4.3. Institutional reproductive success

The number of litters born per year was higher at zoos housing their cheetahs in groups that occur in the wild than at zoos housing their cheetahs in groups that do not occur in the wild. This difference approached significance at the 5% level (Mann-Whitney, $U = 0.0$, $n_1 = 4$, $n_2 = 3$, $p = 0.057$). Institutions housing their cheetahs in groups that do not occur in the wild did not produce any litters between 2008 and 2011 (Table 4.16).

Table 4.16. Institutional breeding success (the number of litters born divided by the sum of the years since 2008 that animals over the age of 2 years were housed at the zoo) and social group type at nine zoos. An asterisk indicates two zoos that frequently exchanged males and females for breeding; the total number of litters born at both zoos was used in the analysis.

Institution	Social group type	Group type occurs in the wild?	Number of litters/year since 2008
Africa Alive! & Banham Zoo*	Singly-housed males and females	Yes	0.75
Chester Zoo	Group-housed males and singly-housed females	Yes	0.33
Marwell Wildlife	Singly-housed males and group-housed females	No	0.00
Paignton Zoo	Singly-housed males and females	Yes	0.50
Paradise Wildlife Park & Wildlife Heritage Foundation*	Singly-housed males, mixed sex adults and group-housed females	No	0.00

Table 4.16. cont.

Institution	Social group type	Group type occurs in the wild?	Number of litters/year since 2008
West Midland Safari Park	Group-housed males and females, mixed sex adults	No	0.00
ZSL Whipsnade Zoo	Group-housed and singly-housed males, singly-housed females	Yes	0.25

4.5. Discussion

The objective of the research presented in this chapter was to compare the behaviour and activity of cheetahs housed in different social groups. It was hypothesised that cheetahs housed in natural social groups (i.e. those that have been observed in wild populations) would display species-specific social behaviours, and those housed in unnatural groups (i.e. those that have not been observed in wild populations) would exhibit behavioural signs of stress, for example pacing behaviour (Wielebnowski, Ziegler *et al*., 2002). The results of behavioural observations showed that males housed in social groups engaged in allogrooming behaviour and few aggressive interactions, as recorded in wild cheetahs. Results therefore support the hypothesis that housing male cheetahs in social groups allows them the opportunity to display the social behaviours that have been observed in their wild counterparts. Pacing behaviour was observed more frequently in cheetahs housed in unnatural-type groups, although this result was not statistically significant. However, no differences were found in the rates of social interactions between natural and unnatural dyads and affiliative behaviour was observed in group-housed females. The hypothesis that cheetahs housed in unnatural groups would exhibit behavioural signs of stress is therefore partially supported by the results of this research.

Further, it was predicted that institutions housing their cheetahs in natural social groups would have better reproductive success than those housing their cheetahs in unnatural social groups (Mellen, 1991). This hypothesis is supported by the analysis of institutional breeding success between 2008 and 2011, which revealed that no litters were born in zoos housing their cheetahs in unnatural-type groups during this period. However, this result should be interpreted with caution due to the small sample size.

Some authors have suggested that housing captive animals in social groups that have been observed in the wild may not always enhance welfare, because the captive environment can vastly differ from the wild (Swaisgood & Schulte, 2010). Thus, research into the behaviour of captive animals housed in social groups is vital. The data presented here show that there are few barriers to replicating natural cheetah social groups in captivity. Group housed males had the opportunity to display the social behaviours observed in wild males, and aggressive encounters were rare. The data also highlight the possible behavioural consequences of housing cheetahs in unnatural-type groups, namely the potential for increased pacing, which might indicate underlying welfare concerns.

Pacing behaviour was observed more frequently among individuals housed in unnatural group types than those housed in groups that have been observed in the wild. Pacing behaviour is of concern because it can indicate welfare problems (Lyons *et al*., 1997; Mason & Latham, 2004; Clubb & Mason, 2007; Mason *et al*., 2007). Stereotypic pacing has been linked to physiological stress, including increased cortisol levels (Wielebnowski, Fletchall *et al*., 2002; Shepherdson *et al*., 2013), and is often observed in situations that result in poor welfare (Mason & Latham, 2004). Thus, pacing behaviour is commonly used as a welfare indicator (Mason & Latham, 2004; Mason *et al*., 2007; Shepherdson *et al*., 2013). It has also been suggested that pacing can have a negative effect on visitors' perceptions of zoological institutions (Miller, 2012), as visitors may interpret abnormal behaviours as the result of poor

husbandry (Rees, 2004). In the present research, pacing was included in the active category of behaviours. However, individuals housed in social groups that would be expected in the wild were more active than those in the other two categories. Thus, even though these individuals were more active, they were engaged in active behaviours other than pacing.

Previous research on the behaviour of zoo felids has suggested that inactivity and stereotypic behaviour are prevalent (Mallapur & Chellam, 2002; Clubb & Mason, 2007; Skibiel *et al*. 2007). In a recent study of 12 cheetahs housed at Fota Wildlife Park (Co. Cork, Ireland), Quirke and O'Riordan (2011) reported mean baseline pacing levels of 13.7% of five-minute scans. In comparison, the cheetahs in the present study were seen pacing on 7.29% (± 1.67%) of one-minute scans. Inactivity is often reported as an undesirable behaviour in zoo felids; however felids in the wild spend the majority of their time inactive (Mellen *et al*., 1998). Indeed, the predominant behaviour recorded in male cheetahs by Caro (1994) was resting. The patterns of inactivity observed in the present research therefore equate to those recorded in wild cheetahs.

No significant effects of visitor numbers were found on the activity of the cheetahs, or on the percentage of visible scans on which pacing behaviour was observed. This is in agreement with previous studies on zoo felids. O'Donovan *et al*. (1993) found no significant effect of visitor presence on the behaviour of female cheetahs, and Margulis *et al*. (2003) found no significant differences in the activity of six felid species (lion; Amur leopard (*Panthera pardus orientalis*); Amur tiger (*Panthera tigris altaica*); snow leopard; clouded leopard; fishing cat (*Felis viverrinus*)) based on the presence or absence of visitors. Visitor effects have been observed primarily in primate species (e.g. Davis *et al*., 2005; Wells, 2005). It may be the case that visitor effects on animal behaviour are less pronounced in other taxa (Margulis *et al*., 2003).

Among group-housed cheetahs, the mean rate of allogrooming was higher than the mean rate of aggression. Interestingly, no differences were found in the rates of social interactions within natural and unnatural dyads. Natural dyads included related and unrelated males, whilst unnatural dyads included related and unrelated females, and mixed-sex adults. However, differences in the rates of social interactions emerged when related and unrelated dyads were examined separately. Thus, it appears that relatedness is an important factor in captive cheetah social interactions, rather than whether or not a particular dyad type would occur in the wild.

The natural social groupings of male cheetahs can be replicated in captivity. Group-housed males frequently groomed one another and shared enclosures successfully, with low rates of aggressive interactions. The welfare benefits of engaging in allogrooming were recently highlighted by Whitham and Wielebnowski (2013), including reduced tension and the affirmation of social bonds. Indeed, Aureli and Yates (2010) found that crested black macaques displayed few aggressive and self-directed behaviours following a grooming bout, and suggested that grooming led to increased social tolerance and the prevention of distress.

Among related males, aggression was observed only at feeding times. These interactions were brief and never prolonged, and often consisted of one or two slaps or bites when food items were thrown over the enclosure fence by the keepers. However, aggression did not occur at every feeding time. For example, on one occasion Moshi and Sifiso (at Port Lympne) shared a large portion of beef with no aggressive interactions. Similar interactions have been observed in wild coalitions around kills. Caro (1994) reported that males slapped or bit each other on 57% of 45 occasions when they were observed eating together, and that aggression was less likely around bigger carcasses than small ones.

Given the importance of sociality in the wild, the ability to house male cheetahs in coalitions in captivity may have positive implications for welfare and reproductive success

(Tetley & O'Hara, 2013). Indeed, the presence of familiar conspecifics can ameliorate the physiological and behavioural effects of environmental stressors (Gust *et al*., 1994; Smith *et al*., 1998; Schaffner & Smith, 2005; Shutt *et al*., 2007; Aureli & Yates, 2010). In previous research, Ruiz-Miranda *et al*. (1998) suggested a degree of psychological attachment between coalition members and used allogrooming behaviour as a measure of evidence of this attachment. In the present study, the rate of allogrooming between sibling males was higher than between non-sibling males, which might be indicative of emotional connectedness between siblings. This result echoes the findings of Ruiz-Miranda *et al*. (1998), who observed increases in vocalisation and pacing when coalition members were separated from one another and increased affiliative behaviours when they were reunited, and the intensity of these behaviours was more pronounced in siblings than non-siblings. These interactions are reminiscent of the intense greeting behaviours observed in fission-fusion species, when sub-groups or individuals reunite following regular – and even brief – periods of separation (e.g. Guinea baboons (*Papio papio*): Whitham & Maestripieri, 2003; African elephants: Leighty *et al*., 2008; hyenas: Smith *et al*., 2011). Reunion-specific behaviours are thought to reaffirm bondedness (or emotional connectedness) between coalition or group members. Whilst cheetahs in the wild do not regularly separate in this way, the Ruiz-Miranda *et al*. (1998) result highlights that the social element between cheetah coalition partners might be more important than previously assumed and should be considered when it is necessary to temporarily isolate captive individuals for management purposes (Tetley & O'Hara, 2013).

Housing male cheetahs in coalitions may have implications for reproductive success. Female reproductive activity may be stimulated in the presence of a group of males (Brown *et al*., 1996; Wielebnowski & Brown, 1998), as most matings observed in the wild have occurred between females and coalition members (Caro, 1993) and ovulation in female cheetahs is often induced (Wildt *et al*., 1993; Caro, 1994; Brown *et al*., 1996; Wielebnowski

& Brown, 1998; Wielebnowski, Ziegler *et al*., 2002). Indeed, Bircher and Noble (1997) reported the use of male-male interactions to stimulate breeding at Saint Louis Zoo (Missouri, USA). Two males were placed in adjacent enclosures and aggressively chased one another along the fence. Two females, in enclosures adjacent to the males, came into oestrus using this technique and one subsequently produced a litter (Bircher & Noble, 1997). Wielebnowski and Brown (1998) found increased oestradiol concentrations in faecal samples of females collected during introductions to males, suggesting that oestrus was detected when males were present. Furthermore, Wielebnowski and colleagues (Wielebnowski, Ziegler *et al*., 2002) observed two separate instances of ovulation in two females in response to the courtship displays of males housed in nearby enclosures. Additionally, Ziegler-Meeks (2009) suggested that coalitions of males are better able to investigate a female's enclosure for signs of oestrus, and they appear more "behaviourally confident" than single males (Ziegler-Meeks 2009, p. 26). Thus, the presence of coalitions in captivity may be important for encouraging natural courtship behaviour in both males and females (Brown *et al*., 1996).

The most striking findings from these data relate to the behaviour of group-housed females. Despite their solitary nature in the wild, very low rates of aggression were observed within female dyads, even less so than within male dyads. Allogrooming between females was also observed, with little difference in the rate of allogrooming within related and unrelated female dyads. Aggressive interactions have been observed following introductions of pairs of females to one another (Wielebnowski, Ziegler *et al*., 2002); however the unrelated females in the present study had been housed together for between two and four years, and it is possible that there were some aggressive interactions following the initial introductions. Wielebnowski and colleagues (Wielebnowski, Ziegler *et al*., 2002) observed no affiliative interactions between unrelated females, and the only affiliative interactions occurred within a mother and daughter dyad. It might be the case that females housed together for long periods

of time, as in the present study, come to show more affiliative behaviours and fewer aggressive interactions. Additionally, some individuals may be behaviourally compatible (Mellen *et al*., 1998; De Rouck *et al*., 2005; Macri & Patterson-Kane, 2011), and adapt well to living in a group.

The results suggest that it is safe for zoos to house compatible groups of females together, which may be necessary where space is limited. However, this is an unnatural social group type for this species. The close proximity of conspecifics can be stressful for asocial species (Jurke *et al*., 1997; Swaisgood & Schulte, 2010). Even those individuals that appear to be behaviourally compatible, displaying little overt aggression, may not reproduce successfully (Kleiman, 1994). Given that the present data also suggest that individuals housed in unnatural groups are likely to show more pacing behaviour, which may be a behavioural sign of stress, housing females in groups should be avoided. Furthermore, there is evidence in the literature that housing female cheetahs in pairs or groups can cause reproductive suppression (Brown *et al*., 1996; Jurke *et al*., 1997; Wielebnowski, Ziegler *et al*., 2002), which is detrimental to the success of captive breeding programmes. The pair-housed females observed by Wielebnowski and colleagues (Wielebnowski, Ziegler *et al*., 2002) exhibited reduced ovarian activity and increased pacing behaviour. Reproductive cycling resumed almost immediately after the females were separated, further emphasising the importance of housing animals in social groups which reflect the groupings of their wild counterparts.

Analysis of institutional breeding success revealed that zoos housing their cheetahs in natural-type social groups were more successful at producing litters than those housing their cheetahs in unnatural groups. Indeed, zoos housing cheetahs in unnatural groups did not produce any litters between 2008 and 2011. This result would appear to support the findings of Wielebnowski and her colleagues (Wielebnowski, Ziegler *et al*., 2002), and other authors who have suggested that housing female cheetahs in pairs or groups can cause reproductive

suppression (Brown *et al*., 1996; Jurke *et al*., 1997). However, only nine institutions were included in the present analysis and only four years of studbook data could be used. The International Cheetah Studbook is published two years in arrears; therefore data on institutional breeding success was only available until 2011. In addition, information on the social housing arrangements at each zoo prior to 2008 was unavailable. This restricted the present analysis to four years of studbook data from nine zoos. Nonetheless, given the difference in reproductive success uncovered by this research, further investigation into the effects of social group housing on institutional breeding success is merited.

There are limitations associated with the methodology used to address the research objectives that are the subject of this chapter. In particular, whilst every effort was made to visit each zoo the same number of times and at different times throughout the year, more field visits were made for behavioural observations during spring and summer months than during winter months. The timing and duration of field visits in this research was constrained by the availability of funds (see Table 4.2 for the schedule of field visits made). Ideally, field visits for behavioural observations would have been balanced across the year, with each zoo visited for the same length of time (see Table 4.1 for the planned data collection schedule). Given that a significant relationship was found between temperature and activity, there may be other seasonal variations in behaviour that were not detected in the present research. However, within the constraints of this study the collection of more data was not feasible. No seasonal effects on reproduction are apparent in wild or captive cheetahs and litters are born throughout the year (Caro, 1994; Brown *et al*., 1996; Marker, Kraus *et al*., 2003; Augustus *et al*., 2006), so the conclusions of the present research are unaffected.

As is often the case with zoo research, management and husbandry routines, coupled with the needs of the animals, restricted the availability of animals for observation at some study sites. Animal welfare remains an important priority, and decisions concerning which

animals had access to on-show enclosures were made by the keeping staff at each study site. During the third visit to Chester Zoo, six days of observation of Adaeze were planned as she had not been on-show on previous visits. However, enclosure maintenance carried out by the keepers meant that she was housed off-show for two days and therefore not visible. Similarly, Kiwara and Zuri at WMSP were temporarily isolated off-show for one day during the first visit. In addition, the decision to split observation time between enclosures at zoos with more than one cheetah enclosure resulted in unequal numbers of hours of observation of each individual. For example, at Paradise Wildlife Park six days of observation were conducted at one enclosure on each visit, whereas at Marwell Wildlife three days of observation were conducted at Enclosure 1 (Suki and Juba) and three days of observation were conducted at Enclosure 2 (Turkus) on each visit. Nonetheless, the total number of observation hours conducted for this research is high in comparison with previously published studies.

4.6. Conclusion

Appropriate social groupings are important for captive animal welfare, as they provide animals the opportunity to engage in species-specific behaviour (Carlstead & Shepherdson, 1994; Ruiz-Miranda *et al*., 1998; De Rouck *et al*., 2005; Price & Stoinski, 2007). Housing animals in groups that would be expected to occur in wild populations can also improve the success of captive breeding programmes (Carlstead & Shepherdson, 1994) and educate zoo visitors about the behaviour of wild animals (Caro, 1993). Research presented in this chapter has shown that housing cheetahs in different social group types can affect their behaviour. The results indicate that male cheetahs can be successfully housed in coalitions, and that housing females in groups should be avoided. A link between social group housing and institutional breeding success was also uncovered; however further research is required into the effects of social group type on breeding success.

The following chapter investigates social interactions among group housed cheetahs in more detail, and presents the results of spatial analyses of social relationships among group housed cheetahs.

5. Association patterns among group-housed cheetahs

5.1. Introduction

5.1.1. Background

Interactions and associations between individuals form the basis of social group structure (Whitehead, 2008a). Results presented in Chapter 4 provided the first quantitative evidence of the effects of social group housing on the behaviour and activity of captive cheetahs. This chapter presents a detailed analysis of spatial relationships among group-housed cheetahs.

Little is currently known about spatial association patterns among captive cheetah groups. Indeed, only one published paper has quantified association in male cheetahs (Chadwick *et al*., 2013). Spatial relationships have, however, been previously studied in wild cheetahs. Caro (1994) observed the behaviour of fifteen coalitions of adult males for 3-hour periods during the middle of the day (0900h to 1700h), over a period of seven years. Males living in coalitions spent more than 70% of five-minute scans within 5m of one another. In coalitions containing littermates and non-relatives, littermates initially spent time in closer proximity with one another rather than their unrelated companion. However, in more established coalitions, these differences were no longer apparent. In contrast, wild adult females are solitary and range over large areas of up to 1,800km^2 (Caro, 1994; Wielebnowski, Ziegler *et al*., 2002; Terio *et al*., 2003; Marker, Dickman *et al*., 2008). The investigation of association patterns among captive female groups is particularly important, since this is an unnatural group type for this species.

Spatial relationships between individuals can be evaluated and quantified by way of an index of association, which estimates the proportion of time individuals in a dyad are seen together (Whitehead, 2008a). The association index, however, masks the extent to which individuals have come into proximity for reasons other than attempting to associate. The

problem of chance associations is more pronounced in a captive environment, where the space available to animals is limited relative to the wild and associations can occur for reasons other than the animals choosing to be together; for example mutual attraction to a food source or gathering at the entrance to indoor accommodation (Stoinski *et al*., 2001). The problem is also evident in multi-zoo studies, where enclosure sizes (and shapes) vary across institutions, making direct comparison of association indices from groups in different zoos difficult.

Stricklin *et al*. (1979) used a computer simulation to examine spacing relationships in square, circular and triangular pens. They investigated the effects of size and shape on the distance to nearest neighbour when the locations of two to five hypothetical animals were randomly generated. Their results demonstrated the effects of pen size and shape on the mean nearest-neighbour distance, with greater distances in the triangle than in the square or the circle when pen size was held constant. Although the study used a different measure of spatial arrangement than the present research (distance to nearest neighbour rather than an index of association), the work highlighted the effects of pen size and shape on spacing arrangements and the importance of adequate pen size in ensuring the welfare of group-housed animals.

Despite the spatial confinement of captive animals rendering their free movement, relative to cage mates, potentially limiting, few attempts have been made to estimate – and thus control for – chance encounters for any species (but see Chadwick *et al*. (2013) and Chadwick *et al*. (under review), which are based on material presented in this chapter). The concern for overestimating association may not only be limited to captive animals since free-ranging animals, for example animals in managed areas (e.g. sanctuaries or reserves), may have restricted ranges. Indeed, animals in totally wild environments may also be naturally limited in their ranging; for example, territorial species, where an individual's or group's movement may be restricted by the presence of conspecific neighbours.

This chapter presents a new method for correcting indices of association to take into account chance encounters, and investigates indices of association among group-housed cheetahs.

5.1.2. Objective and hypothesis

This chapter aims to address Objective 2 of the research:

- *To investigate spatial association in group-housed cheetahs.*

Evidence from the wild suggests that coalitions of males remain in close proximity to one another, move around their territories together, and display affiliative behaviours (Caro, 1994; Gottelli *et al*., 2007). There is also evidence that stronger associations are formed between related individuals than between unrelated individuals, both in the wild (Caro, 1994) and in captivity (Ruiz-Miranda *et al*., 1998; Chadwick *et al*., 2013). In contrast, wild females are solitary and adult females do not form social groups (Caro, 1994; Wielebnowski, Ziegler *et al*., 2002; Terio *et al*., 2003). Thus, it is hypothesised that males housed in groups in captivity will maintain close proximity to one another; related males will be more closely associated than unrelated males; and that weak associations will be found among group-housed captive females.

Objective 2 is investigated using indices of association and Geographic Information Systems (GIS) to analyse spatial data on the locations of group housed cheetahs. A simple Monte Carlo simulation was devised to estimate the effects of enclosure size and shape on the probability of chance encounters among dyads. Information from the simulation was used to correct indices of association calculated from field observations, thereby taking into account the effect of chance encounters on the observed associations.

5.1.3. Outline of the chapter

A review of the literature relevant to this chapter is presented in Chapter 2; information on cheetah social organisation in the wild is presented in Sub-section 2.6.1 and on captive cheetah groups in Sub-section 2.6.2. Background information on the methods used in this chapter is presented in Chapter 3. Section 3.3 reviews the use of indices of association in studies of wild and captive animals and a review of the use of GIS in studies of animal behaviour is presented in Section 3.4.

Section 5.2 of this chapter describes the detailed procedures used to collect the data required to address Objective 2. The simulation used to calculate chance encounters and produce corrected indices of association is described in Section 5.2.3. Section 5.3 presents the results, divided into sub-sections on the results of the simulation (Sub-section 5.3.1) and the results of field observations (Sub-section 5.3.2). Finally, Section 5.4 discusses the findings of spatial analyses and presents a critical analysis of the methodological approach.

5.2. Procedures

5.2.1. Collection of location data

Location data were collected on group housed individuals at Chester Zoo, Exmoor Zoo, Port Lympne, West Midland Safari Park and ZSL Whipsnade Zoo. Location data were not collected at Africa Alive!, Banham Zoo, Paignton Zoo or Wildlife Heritage Foundation as each of them housed solitary animals.

Location data were collected at the same time as behavioural data. Procedures for behavioural data collection can be found in Sub-section 4.2.2 of Chapter 4. During scan sampling and instantaneous recording of behaviour, the position of each individual in the enclosure was also recorded using a scan sampling technique. Locations were recorded once every ten minutes onto maps of the enclosure, in order to determine the proximity of each

cheetah to the others (Crockett & Ha, 2010; Blowers *et al*., 2012). An enclosure map was provided by Chester Zoo (Figure 5.1) and a sketch map was drawn at Exmoor Zoo (Figure 5.2). Elsewhere, printouts of aerial photographic images of the enclosures (Google Earth, 2012) were used to record location data (Port Lympne, Figure 5.3 and Figure 5.4; West Midland Safari Park, Figure 5.5; ZSL Whipsnade Zoo, Figure 5.6). The maps and images detailed the locations of landmarks in the enclosures (e.g. trees, shelters, platforms and gates) and the positions of the cheetahs were recorded in relation to these landmarks.

The location of each individual was marked on the map using his or her initial, followed by the number of the corresponding sample point. Forty-two 10-minute sample points were contained within a seven-hour observation period, so locations were numbered consecutively between 1 and 42. This method of recording locations not only resulted in a record of each cheetah's position within the exhibit, but also produced a chronological sequence of their movements around the enclosure.

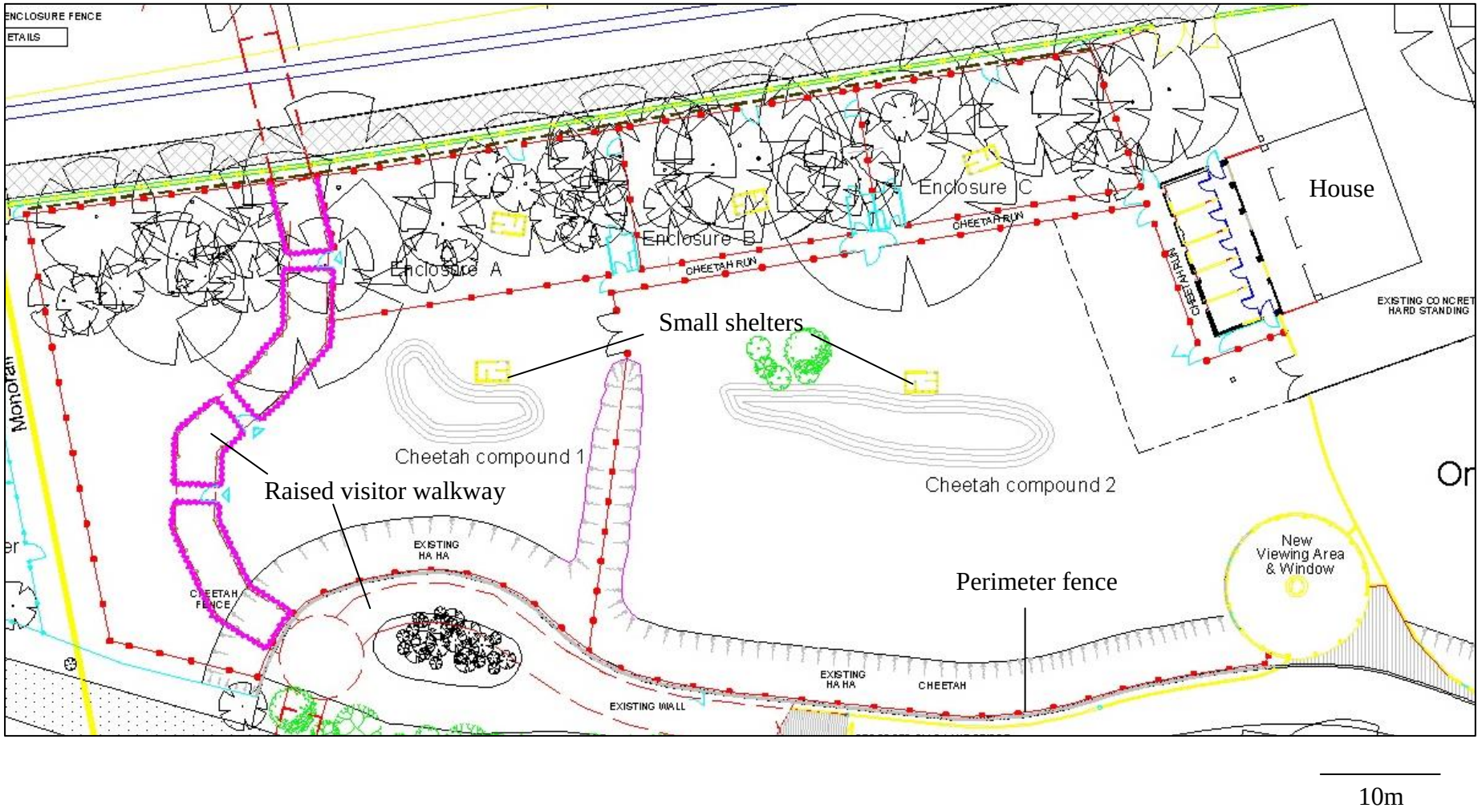

Figure 5.1. Map of the cheetah exhibit provided by Chester Zoo.

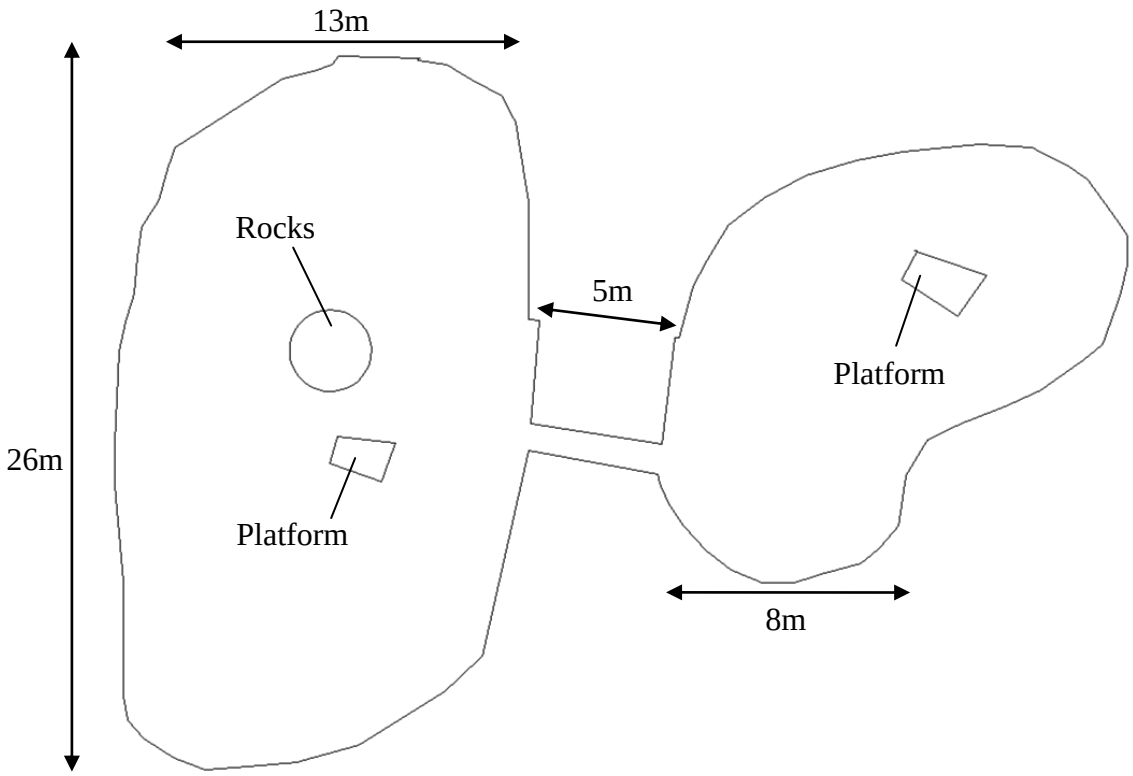

Figure 5.2. Sketch map of the cheetah enclosure at Exmoor Zoo.

Figure 5.3. Aerial photographic image of Enclosure 1 at Port Lympne. Related males Moshi and Sifiso were housed in this enclosure (source: Google Earth, 2012).

Figure 5.4. Aerial photographic image of Enclosure 2 at Port Lympne. Related females Izzy and Split were housed in this enclosure and had access to both sections via an open gate (source: Google Earth, 2012).

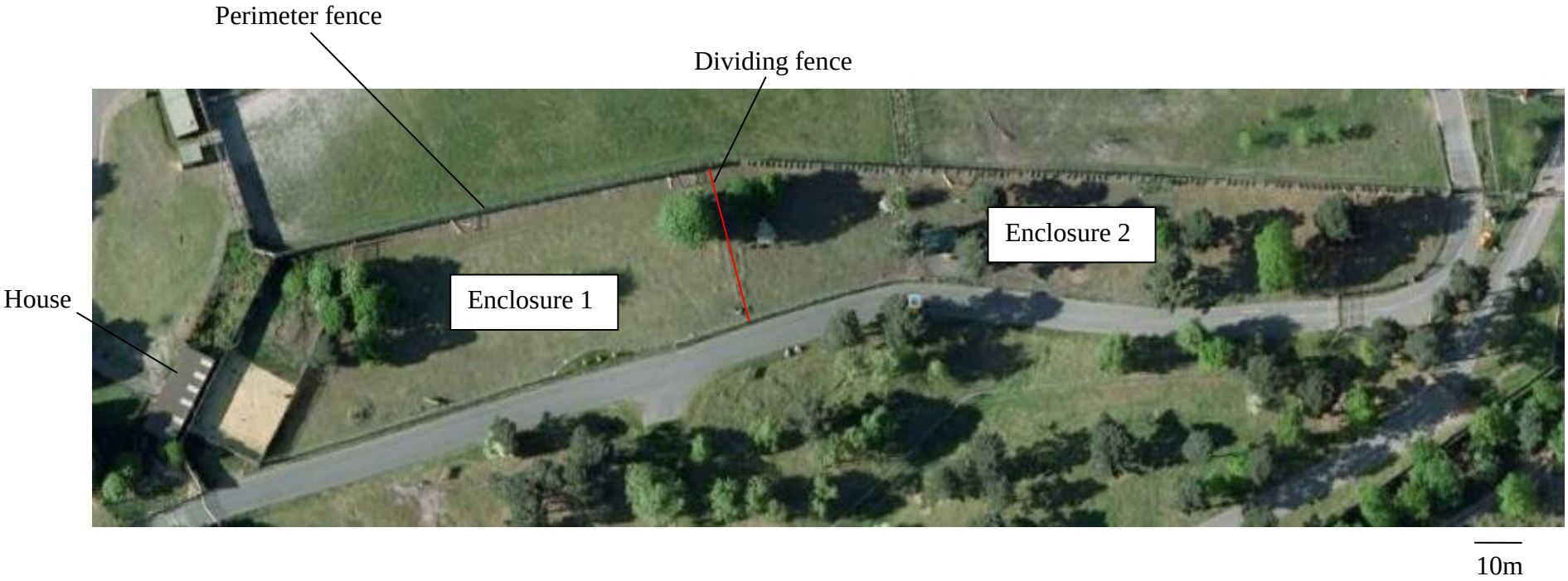

Figure 5.5. Aerial photographic image of the cheetah reserve at West Midland Safari Park (source: Google Earth, 2012).

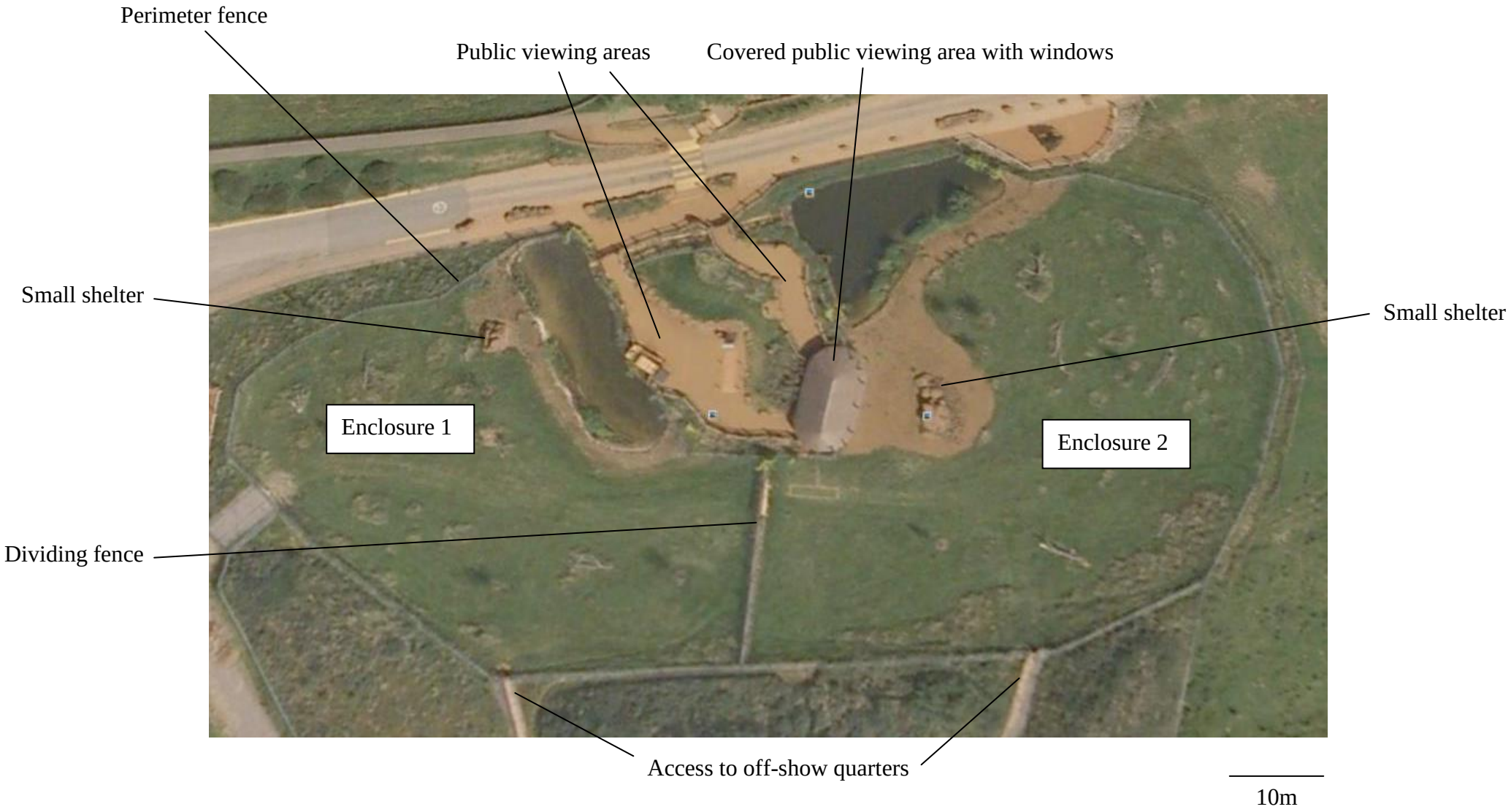

Figure 5.6. Aerial photographic image of the cheetah enclosure at ZSL Whipsnade Zoo (source: Google Earth, 2012).

5.2.2. Analysis of location data

Ordnance Survey MasterMap™ data for each enclosure were downloaded using the EDINA Digimap Ordnance Survey Service (http://edina.ac.uk/digimap). The enclosure maps and aerial photographic images of the enclosures on which recordings were made were geo-corrected using ERDAS Imagine® 2010. Geo-correction relates the co-ordinates of image pixels to spatial co-ordinates obtained from the MasterMap™ data, and allows images to be displayed in a Geographic Information System with the correct scaling and orientation. The geo-corrected images were then imported into ESRI (Environmental Systems Resource Institute) ArcGIS™ 9.3.1, along with the Ordnance Survey MasterMap™ data, and vector-based polygons were digitised representing the boundaries of each enclosure. Every location point for each cheetah was digitised to create a point data set within the GIS (Figures 5.7 – 5.13). Since the polygons representing the enclosure boundaries were combined with the Ordnance Survey data in the GIS, every digitised point had British National Grid co-ordinates and the distances between them could be calculated.

The co-ordinates of each location point in the GIS were used to calculate the distances between individuals in the same enclosure, on every 10-minute sample point, in metres. If the location of animal A in two-dimensional space is x_a, y_a and the location of animal B is x_b, y_b, the Euclidean distance between these points is calculated using Pythagoras' Theorem (Equation 5.1). If this value (d) is less than the maximum distance (m) which defines association ($d < m$) then the animals will be deemed to be associating together. So, if $m = 5$ units and $d = 7$ units, the animals are not associating; if $d = 0.5$ units, then they are associating.

$$\text{Distance } (d) = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2} \qquad \text{Equation 5.1}$$

Indices of association (I_A) for every dyad in each enclosure were then calculated using the simple ratio index (Equation 5.2: Ginsberg & Young, 1992), where x is the number of separate occasions when animals A and B are observed together, y_A is the number of separate occasions when only A is observed, y_B is the number of separate occasions when only B is observed and y_{AB} is the number of separate occasions when A and B are observed not associated. Here, 'separate occasions' were defined as recordings of proximity made at 10-minute intervals and two individuals were 'together' when the distance between them was 5m or less (Caro, 1994).

$$I_A = \frac{x}{(x + y_{AB} + y_A + y_B)} \qquad \text{Equation 5.2}$$

The use of the simple ratio index was justified in this instance because its four assumptions, outlined by Whitehead (2008a), were met:

1. Recorded associations were a symmetric one-zero measure of whether the members of a dyad were or were not associated in a sampling period.
2. Recorded associations were accurate.
3. If one individual was identified in a sampling period, then all its associates were identified.
4. Members of a dyad were equally likely to be identified whether they were associated or not.

Location recordings were made for 22 different pairs of cheetahs. Where individuals had access to different enclosures during the study (at Chester Zoo and West Midland Safari Park), separate indices of association were calculated for each dyad for each enclosure size. Thus, 43 indices of association were calculated in total. Mann-Whitney U tests were used to

examine differences in indices of association between male and female dyads and related and unrelated dyads.

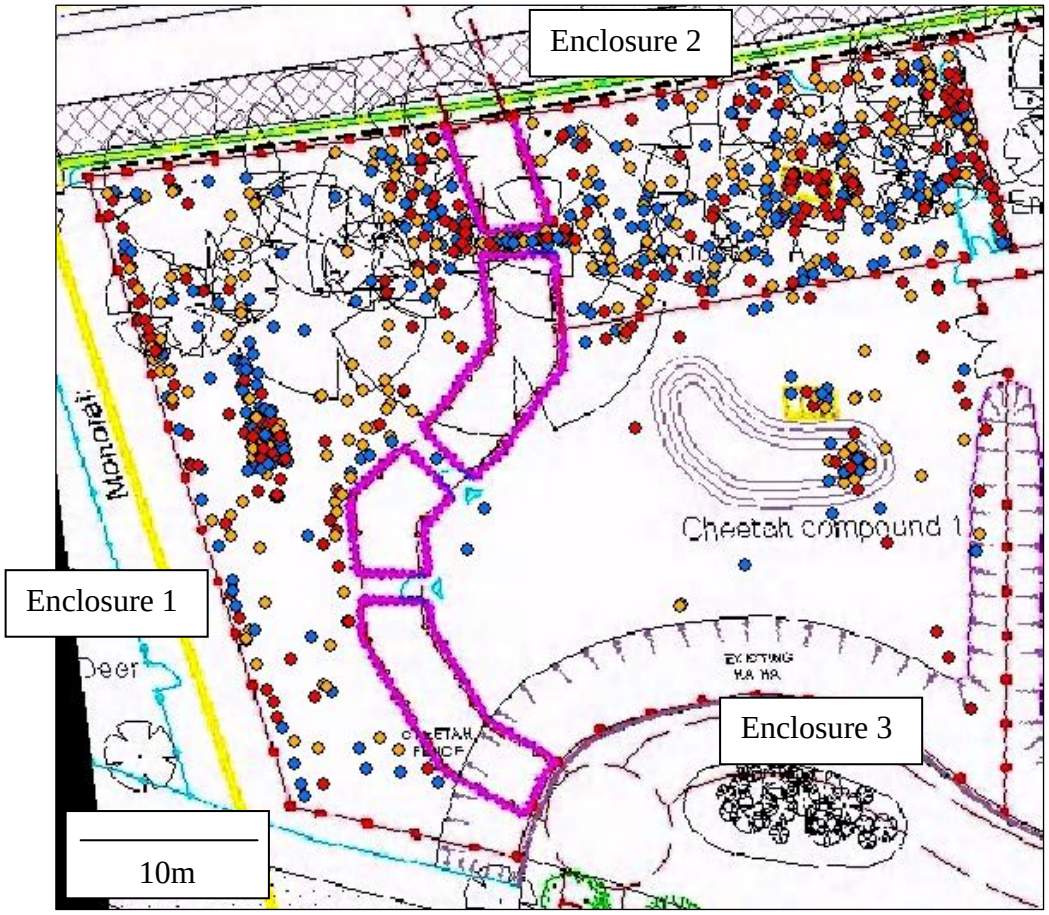

Figure 5.7. Locations of related males Burba (orange), Singa (blue) and unrelated male Matrah (red) at Chester Zoo. The group had access to four combinations of Enclosures 1, 2 and 3 during the course of field observations: 143 recordings were made when the group were housed in Enclosure 1 only; 291 in Enclosures 1 and 2; 35 in Enclosures 1 and 3; 17 when they were housed in Enclosure 3 only.

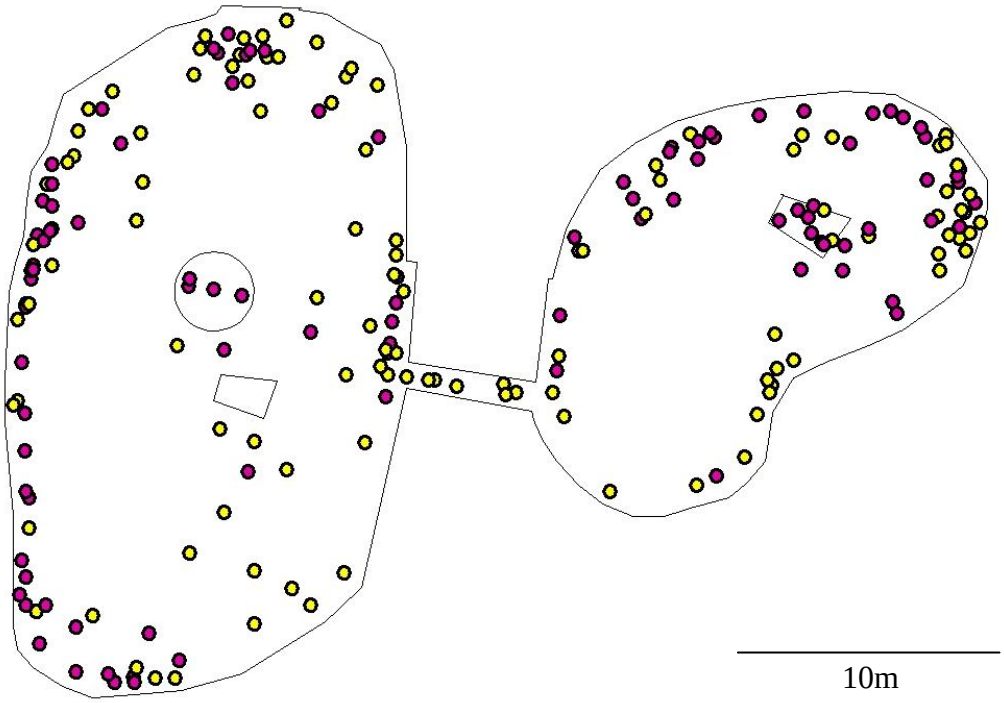

Figure 5.8. Locations of Dave (yellow) and his sister Nina (pink) at Exmoor Zoo. 254 recordings were made of this dyad.

Figure 5.9. Locations of related males Moshi (red) and Sifiso (green) in Enclosure 1 at Port Lympne. 122 recordings were made of this dyad.

Figure 5.10. Locations of related females Izzy (green) and Split (pink) in Enclosure 2 at Port Lympne. 81 recordings were made of this dyad.

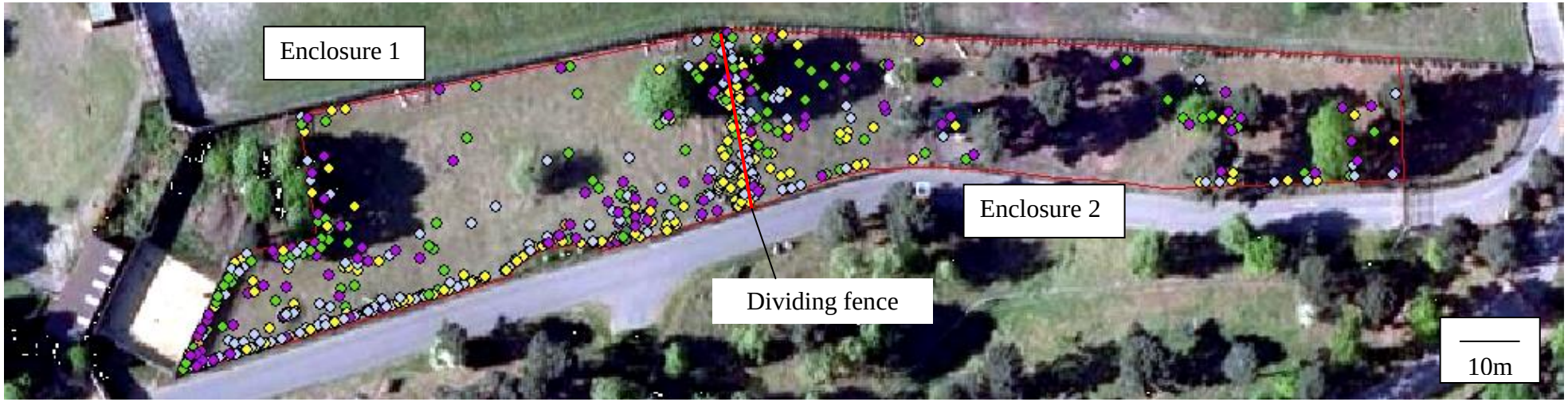

Figure 5.11. Locations of related males Munya (purple) and Belika (green), and unrelated males Cheetor (yellow) and Duma (blue) at West Midland Safari Park. 114 recordings were made when the group was housed in Enclosure 1 and 182 were made when they were housed in Enclosure 2.

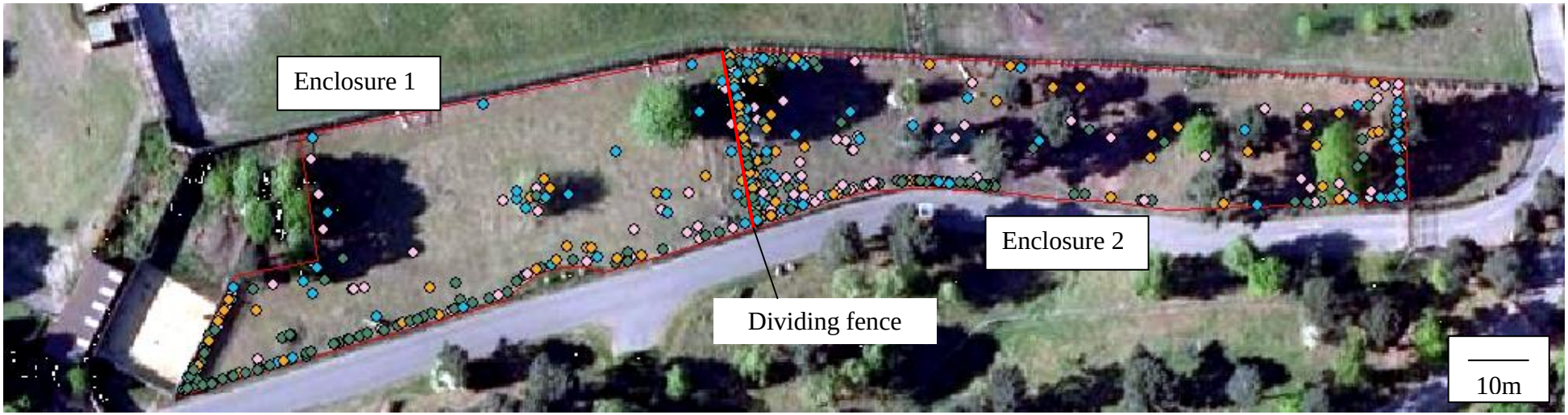

Figure 5.12. Locations of related females Epesi (green) and Azizi (orange), and unrelated females Kiwara (pink), Zuri (blue) at West Midland Safari Park. 110 recordings were made when the group was housed in Enclosure 1 and 192 were made when they were housed in Enclosure 2.

Figure 5.13. Locations of unrelated males Maktoum (blue), Al Safa (yellow) in Enclosure 1, and related males Jake (pink), Brooke (green) and Oscar (purple) in Enclosure 2 at ZSL Whipsnade Zoo. 281 recordings were made of Maktoum and Al Safa and 213 were made of Jake, Brooke and Oscar.

Analyses of social behaviour should not only take into account spatial proximity, but also behavioural interactions (Whitehead & Dufault, 1999). Allogrooming has been observed in wild male coalitions (Caro, 1993, 1994) and can indicate psychological attachment between individuals (Ruiz-Miranda *et al*., 1998). Thus, rates of allogrooming per visible hour were compared with indices of association for each dyad, to investigate whether individuals interacted with each other, rather than simply being observed in proximity to one another. Rates of allogrooming were calculated by dividing the number of occurrences of allogrooming within the dyad by the number of hours both members of the dyad were visible. Spearman's rank-order correlation coefficient was used to examine the relationship between corrected indices of association and rates of allogrooming and aggression.

5.2.3. Generation of random points

To ascertain the effects of area and shape on the probability of chance encounters, a simple Monte Carlo simulation was devised (Chadwick *et al*., 2013; Chadwick *et al*., under review). In Monte Carlo methods, data are repeatedly sampled from simulated, random distributions and are used to estimate test statistics or to test a statistical method (Crowley, 1992; Field, 2013). In the present research, the simulation was used to generate 200 pairs of random points within hypothetical shapes measuring between 20 units^2 and 10,000 units^2. This equated to 200 observations and was considered to represent a reasonable sampling effort in a field study. Random points were generated in squares, rectangles, circles and actual enclosure shapes to investigate the effects of area and shape on the probability of chance encounters (Chadwick *et al*., under review).

For squares and rectangles, a simple simulation was devised in Microsoft® Excel 2007. The simulation consisted of a spreadsheet containing six columns (Figure 5.14). Cells A2 and A3 contained the dimensions of the shape and represented the maximum random

value that could be generated in the four columns. This effectively defined the boundaries of the shape. For squares, these cells contained the square root of the area of the square. For rectangles, one dimension was fixed at ten units and the second was varied so that the area of each rectangle equalled the area of the corresponding square. Cell A1 contained the intra-dyad distance criterion that defined an association. The effect of changing the criterion for association was investigated in squares of different sizes by altering this value. Columns C – F contained randomly generated numbers, representing the x, y co-ordinates of the pairs of points. Formulae in column G calculated the distances between the points, and in column H whether or not they were associated based on the distance criterion.

	A	B	C	D	E	F	G	H
1	5	distance criterion	x_a	y_a	x_b	y_b	distance	associated?
2	10	max x value	=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C2-E2)^2+(D2-F2)^2)	=IF(G2<=$A$1,"1","0")
3	10	max y value	=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C3-E3)^2+(D3-F3)^2)	=IF(G3<=$A$1,"1","0")
4	=A2*A3	area	=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C4-E4)^2+(D4-F4)^2)	=IF(G4<=$A$1,"1","0")
5			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C5-E5)^2+(D5-F5)^2)	=IF(G5<=$A$1,"1","0")
6			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C6-E6)^2+(D6-F6)^2)	=IF(G6<=$A$1,"1","0")
7			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C7-E7)^2+(D7-F7)^2)	=IF(G7<=$A$1,"1","0")
8			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C8-E8)^2+(D8-F8)^2)	=IF(G8<=$A$1,"1","0")
9			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C9-E9)^2+(D9-F9)^2)	=IF(G9<=$A$1,"1","0")
10			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C10-E10)^2+(D10-F10)^2)	=IF(G10<=$A$1,"1","0")
11			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C11-E11)^2+(D11-F11)^2)	=IF(G11<=$A$1,"1","0")
12			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C12-E12)^2+(D12-F12)^2)	=IF(G12<=$A$1,"1","0")
13			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C13-E13)^2+(D13-F13)^2)	=IF(G13<=$A$1,"1","0")
14			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C14-E14)^2+(D14-F14)^2)	=IF(G14<=$A$1,"1","0")
15			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C15-E15)^2+(D15-F15)^2)	=IF(G15<=$A$1,"1","0")
16			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C16-E16)^2+(D16-F16)^2)	=IF(G16<=$A$1,"1","0")
17			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C17-E17)^2+(D17-F17)^2)	=IF(G17<=$A$1,"1","0")
18			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C18-E18)^2+(D18-F18)^2)	=IF(G18<=$A$1,"1","0")
19			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C19-E19)^2+(D19-F19)^2)	=IF(G19<=$A$1,"1","0")
20			=RAND()*$A$2	=RAND()*$A$3	=RAND()*$A$2	=RAND()*$A$3	=SQRT((C20-E20)^2+(D20-F20)^2)	=IF(G20<=$A$1,"1","0")

Figure 5.14. Excerpt from the Microsoft® Excel spreadsheet used to simulate chance encounters within squares and rectangles.

For the actual enclosure shapes, the 'Generate Random Points' tool, found in Hawth's Analysis Tools for ArcGIS™ (Beyer, 2004), was used. Random points were generated within the spatially referenced polygons of the cheetah enclosures at Chester Zoo, Exmoor Zoo, Port Lympne, West Midland Safari Park and ZSL Whipsnade Zoo. Circles and squares of the same areas were also digitised in ArcGIS™ and spatially referenced using the same co-ordinate

system as the actual enclosures. Points were generated in square shapes using this tool for comparison with the Excel simulation. Two hundred pairs of random points were generated within each shape.

Both methods of random point generation assume that resources are evenly distributed throughout the area; that animals make use of the whole area and that each consecutive location plotted for each individual in the dyad is independent of the previous location.

5.2.4. Calculating chance encounters

The probability of a chance encounter was calculated by dividing the number of associations by the number of pairs of points (200). The simulation was repeated 1000 times for each shape (as Bejder *et al*., 1998) and the mean probability of a chance encounter (and standard deviation) was calculated. Since the data were normally distributed, independent t-tests were used to examine differences in the probability of a chance association:

1) when points were generated in square shapes using Excel and GIS
2) between squares and circles of the same area
3) between squares and rectangles of the same area
4) between actual zoo enclosures and squares of the same area.

Due to the large number of replicates (n = 1000), there was the potential for very small effects (differences) to be statistically significant, resulting in a Type I error (Field, 2013). Thus, the effect size (r) was also calculated (Equation 5.3), where t is the test statistic and df is the degrees of freedom (Cohen, 1992; Field, 2013). Following Cohen (1992), an effect size of 0.1 was considered to represent a small effect (no difference), 0.3 a medium effect and 0.5 a

large effect (an actual difference) of the method of random point generation or shape on the probability of a chance encounter.

$$r = \sqrt{\frac{t^2}{t^2 + df}}$$ Equation 5.3

5.2.5. Correcting observed indices of association

Monte Carlo simulations have been previously used in studies of wild animals to test whether or not individuals have preferred associates (e.g. Bejder *et al*., 1998; Gillam *et al*., 2011; Carter *et al*., 2013) by producing randomly generated data sets for comparison with real data sets. Thus, further simulations using the GIS were conducted in which the number of pairs of points generated equalled the actual number of observations made in that part of the field study to which the calculated association index was compared. For example, when Burba and Singa were studied in Enclosure 1 at Chester Zoo, the association index was calculated from 143 recordings, so the simulation was used to generate 143 pairs of random locations. The distances between these locations were used to calculate an association index for chance encounters. The simulation was replicated 1000 times and the mean index of association (and standard deviation) was calculated. This was repeated for every dyad in the study. The observed index of association for each dyad was then corrected by subtracting the relevant mean index of association calculated by simulation (Chadwick *et al*., 2013). The corrected index of association took into account chance encounters and allowed comparisons to be made between dyads housed in different enclosures.

5.3. Results

5.3.1. The effects of area and shape on the probability of a chance encounter

Statistically significant differences were found in the probability of a chance encounter when Excel and GIS were used to generate random points within square shapes (Table 5.1). However, although the results of some of the t-tests were statistically significant, effect sizes were small and ranged from 0.01 to 0.13 (Table 5.1). Thus, there was no actual difference in the probability of a chance encounter when Excel and GIS were used to generate random points within squares for any of the areas tested (Figure 5.15).

Table 5.1. Results of independent t-tests on the differences in the probability of a chance encounter in square shapes, when random points were generated using Geographic Information Systems and Microsoft® Excel. The distance criterion was fixed at 5 units.

	Probability of a chance encounter $\overline{x}$ (σ)		Independent t-test results (df = 1998)		
Area (units^2)	GIS	Excel	t	p	*r*
20	0.994 (0.005)	0.994 (0.005)	-2.46	0.014	0.05
30	0.937 (0.017)	0.937 (0.018)	-0.33	0.739	0.01
40	0.841 (0.026)	0.841 (0.026)	-0.29	0.775	0.01
50	0.759 (0.029)	0.752 (0.030)	5.32	0.000	0.12
100	0.493 (0.034)	0.483 (0.037)	5.92	0.000	0.13
200	0.288 (0.032)	0.283 (0.031)	3.18	0.001	0.07
400	0.157 (0.025)	0.155 (0.024)	2.14	0.032	0.05
500	0.131 (0.024)	0.129 (0.024)	1.77	0.077	0.04
600	0.112 (0.022)	0.109 (0.022)	2.63	0.009	0.06
750	0.091 (0.021)	0.089 (0.020)	1.30	0.194	0.03
800	0.084 (0.019)	0.083 (0.019)	0.58	0.565	0.01
1000	0.069 (0.018)	0.069 (0.019)	0.57	0.566	0.01
1500	0.048 (0.015)	0.047 (0.015)	1.24	0.216	0.03
2000	0.037 (0.013)	0.036 (0.013)	2.67	0.008	0.06

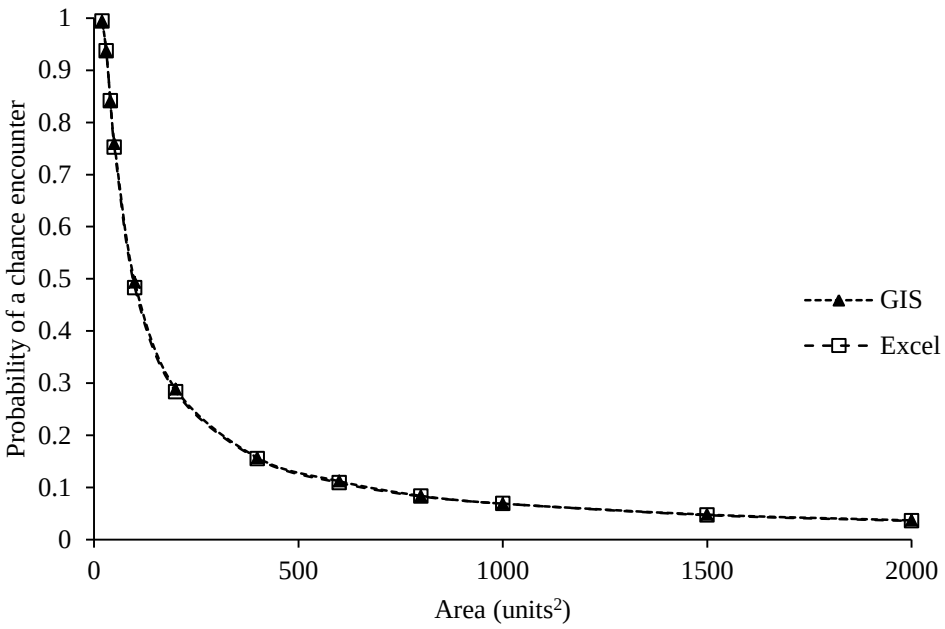

Figure 5.15. Probability of a chance encounter in square shapes ranging from 20 units^2 to 2000 units^2, when points were generated using Geographic Information Systems and Microsoft® Excel. The distance criterion was fixed at 5 units. Due to the similarity of the results obtained using both methods, the two lines appear concurrent.

The probability of a chance encounter was significantly higher in a circle measuring 20 units^2 than in a square of the same area ($t_{1998} = 37.38$, $p<0.001$, $r = 0.64$). This represented a large effect of shape on the probability of a chance encounter. Significant differences representing a medium effect were found in enclosures of 30 units^2 ($t_{1998} = 17.97$, $p<0.001$, $r = 0.37$) and 40 units^2 ($t_{1998} = 16.44$, $p<0.001$, $r = 0.35$). No significant differences with effect sizes greater than 0.2 were found in areas larger than 50 units^2 (Table 5.2; Figure 5.16).

Table 5.2. Results of independent t-tests on the differences in the probability of a chance encounter in circles and squares, when random points were generated using Geographic Information Systems. The distance criterion was fixed at 5 units.

	Probability of a chance encounter $\overline{x}$ (σ)		Independent t-test results (df = 1998)		
Area (units^2)	Circle	Square	t	p	*r*
20	1.000 (0.000)	0.994 (0.005)	37.38	0.000	0.64
30	0.950 (0.016)	0.937 (0.017)	17.97	0.000	0.37
40	0.859 (0.024)	0.841 (0.026)	16.44	0.000	0.35
50	0.771 (0.029)	0.759 (0.029)	8.94	0.000	0.20
100	0.498 (0.036)	0.493 (0.034)	3.01	0.003	0.07
200	0.288 (0.032)	0.288 (0.032)	0.61	0.543	0.01
400	0.161 (0.025)	0.157 (0.025)	3.56	0.000	0.08
500	0.131 (0.023)	0.131 (0.024)	-0.53	0.599	0.01
600	0.111 (0.023)	0.112 (0.022)	-0.42	0.673	0.01
750	0.093 (0.020)	0.091 (0.021)	2.07	0.039	0.05
800	0.086 (0.020)	0.084 (0.019)	2.78	0.005	0.06
1000	0.071 (0.018)	0.069 (0.018)	1.68	0.092	0.04
1500	0.047 (0.015)	0.048 (0.015)	-1.41	0.159	0.03
2000	0.036 (0.013)	0.037 (0.013)	-2.64	0.008	0.06

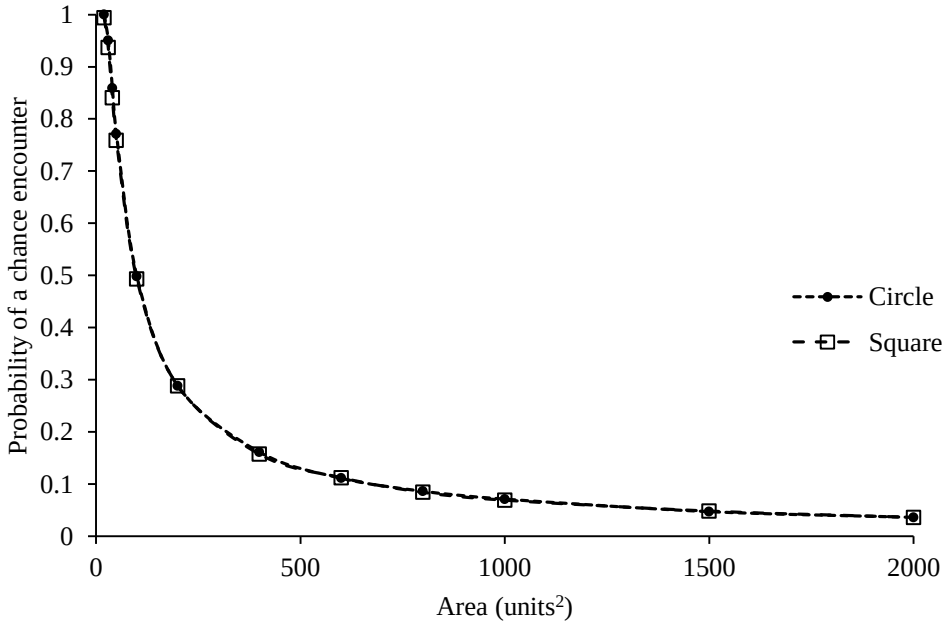

Figure 5.16. Probability of a chance encounter in circles and squares ranging from 20 units^2 to 2000 units^2. The distance criterion was fixed at 5 units. Due to the similarity of the results obtained for both shapes, the two lines appear concurrent.

The same trend was apparent in rectangular shapes, where one dimension was fixed at 10 units (Figure 5.17). The probability of a chance encounter was significantly higher in rectangles measuring 25 units^2 (t_{1998} = 238.05, p<0.001, r = 0.98), 36 units^2 (t_{1998} = 125.39, p<0.001, r = 0.94) and 49 units^2 (t_{1998} = 43.58, p<0.001, r = 0.70) than in squares of the same area (Figure 5.18; Table 5.3). No significant differences with effect sizes greater than 0.23 were found in larger areas (Table 5.3).

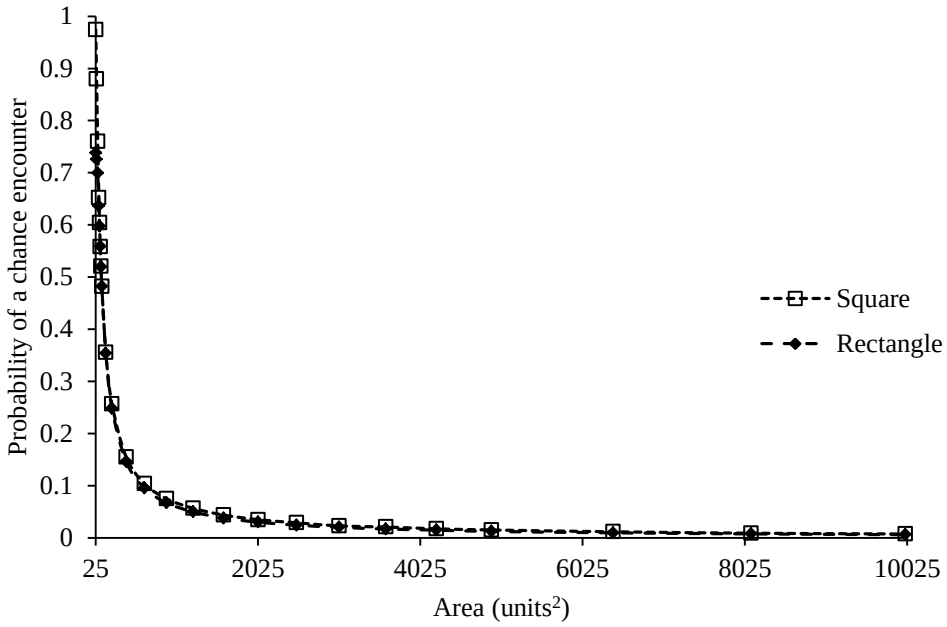

Figure 5.17. Probability of a chance encounter in squares and rectangles of the same area with one dimension fixed at 10 units, ranging from 25 units^2 to 10000 units^2. The distance criterion was fixed at 5 units. Due to the similarity of the results obtained for both shapes, the two lines appear concurrent.

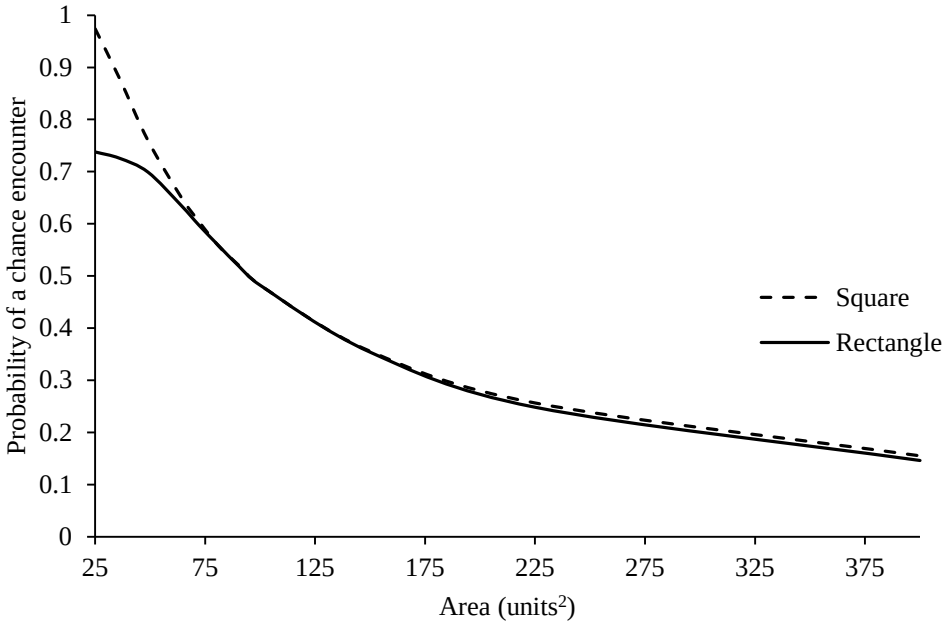

Figure 5.18. Probability of a chance encounter in squares and rectangles of the same area with one dimension fixed at 10 units, ranging from 25 units^2 to 400 units^2. The distance criterion was fixed at 5 units.

Table 5.3. Results of independent t-tests on the differences in the probability of a chance encounter in squares and rectangles of the same area, with one dimension fixed at 10 units. The distance criterion was fixed at 5 units.

	Probability of a chance encounter $\overline{x}$ (σ)		Independent t-test results (df = 1998)		
Area (units^2)	Square	Rectangle	t	p	*r*
25	0.974 (0.011)	0.738 (0.029)	238.05	0.000	0.98
36	0.880 (0.023)	0.726 (0.031)	125.39	0.000	0.94
49	0.760 (0.030)	0.699 (0.032)	43.58	0.000	0.70
64	0.652 (0.033)	0.636 (0.034)	10.77	0.000	0.23
81	0.558 (0.034)	0.559 (0.035)	-0.51	0.611	0.01
100	0.482 (0.035)	0.482 (0.035)	-	-	-
225	0.256 (0.031)	0.248 (0.031)	5.97	0.000	0.13
400	0.155 (0.026)	0.146 (0.026)	7.78	0.000	0.17
625	0.104 (0.021)	0.095 (0.021)	8.92	0.000	0.20
900	0.075 (0.018)	0.067 (0.018)	9.52	0.000	0.21
1225	0.057 (0.016)	0.050 (0.015)	9.93	0.000	0.22
1600	0.044 (0.014)	0.038 (0.013)	9.53	0.000	0.21
2025	0.035 (0.013)	0.030 (0.012)	8.39	0.000	0.18
2500	0.029 (0.012)	0.024 (0.011)	8.99	0.000	0.20
3025	0.023 (0.010)	0.020 (0.010)	5.98	0.000	0.13
3600	0.021 (0.010)	0.017 (0.009)	9.10	0.000	0.20
4225	0.017 (0.009)	0.015 (0.008)	6.60	0.000	0.15
4900	0.015 (0.009)	0.012 (0.008)	7.85	0.000	0.17
6400	0.012 (0.007)	0.010 (0.007)	6.32	0.000	0.14
8100	0.009 (0.007)	0.007 (0.006)	4.62	0.000	0.10
10000	0.007 (0.006)	0.006 (0.005)	5.27	0.000	0.12

There were no significant differences with large effect sizes in the probability of a chance encounter between actual enclosure shapes and squares of the same area (Table 5.4). The only significant differences with effect sizes greater than 0.1 were found in enclosures whose shapes were drastically different from regular geometric shapes (Chester 1, Chester 1 & 2, Chester 1 & 3, Figure 5.7; Exmoor, Figure 5.8) and this still only represented a small effect.

Table 5.4. Results of independent t-tests on the probability of a chance encounter in actual enclosures and in squares of the same area. The distance criterion was fixed at 5 units.

		Probability of a chance encounter $\overline{x}$ (σ)		Independent t-test results (df = 1998)		
Enclosure	Area (m^2)	Actual Shape	Square	t	p	*r*
Chester 1	497.06	0.117 (0.023)	0.130 (0.025)	-12.09	0.000	0.26
Chester 1 & 2	784.82	0.075 (0.019)	0.086 (0.019)	-13.00	0.000	0.28
Chester 1 & 3	1187.21	0.053 (0.015)	0.058 (0.017)	-6.81	0.000	0.15
Chester 3	690.15	0.094 (0.020)	0.096 (0.022)	-1.71	0.088	0.04
Exmoor	643.06	0.095 (0.020)	0.103 (0.021)	-8.41	0.000	0.18
Port Lympne 1	2812.71	0.026 (0.011)	0.026 (0.011)	-1.10	0.270	0.02
Port Lympne 2	2983.85	0.025 (0.012)	0.024 (0.011)	0.70	0.483	0.02
WMSP 1	2925.51	0.024 (0.011)	0.024 (0.011)	-0.39	0.694	0.01
WMSP 2	2752.97	0.025 (0.011)	0.026 (0.011)	-1.22	0.222	0.03
Whipsnade 1	1693.08	0.042 (0.014)	0.041 (0.015)	0.35	0.725	0.01
Whipsnade 2	2268.54	0.032 (0.012)	0.032 (0.012)	-0.17	0.867	0.00

As would be expected, increasing the distance criterion that defined association through 1 unit to 10 units resulted in an increase in the probability of a chance encounter (Figure 5.19).

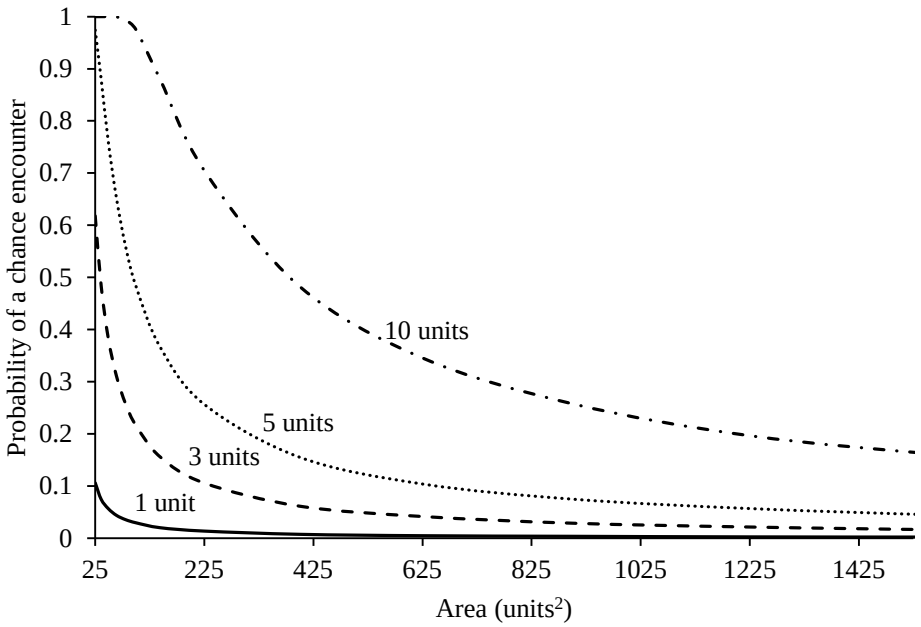

Figure 5.19. The effect of altering the distance criterion on the probability of a chance encounter in square shapes ranging from 25 units^2 to 1425 units^2.

5.3.2. Corrected indices of association and cheetah social behaviour

Observed indices of association calculated from the field study were significantly higher than those calculated using chance encounters (Mann-Whitney, U = 84.0, $n_1 = n_2 = 43$, $p<0.001$). The results of the GIS simulation were used to correct the observed indices of association and are presented in Table 5.5. The index of association calculated from chance encounters was subtracted from the observed index of association to give a corrected index of association for each dyad. Corrected indices of association for all dyads are presented in Figures 5.21 – 5.25.

Table 5.5. Indices of association based on chance encounters, calculated from the GIS simulation, and observed indices of association for each enclosure.

Enclosure	Enclosure area (m^2)	No. of observations	I_A calculated from simulation	Range of observed I_As
Chester 1	467.06	143	0.122	0.594-0.636
Chester 1 & 2	784.82	291	0.077	0.519-0.605
Chester 1 & 3	1187.21	35	0.054	0.600-0.714
Chester 3	690.15	17	0.096	0.529-0.941
Exmoor	643 .06	254	0.098	0.512
Port Lympne 1	2812.71	122	0.027	0.463
Port Lympne 2	2983.85	81	0.025	0.565
WMSP 1 (females)	2925.51	110	0.025	0.054-0.240
WMSP 1 (males)	2925.51	114	0.022	0.043-0.447
WMSP 2 (females)	2752.97	192	0.026	0.177-0.328
WMSP 2 (males)	2752.97	182	0.023	0.077-0.330
Whipsnade 1	1693.08	281	0.043	0.349
Whipsnade 2	2268.54	213	0.033	0.878-0.920

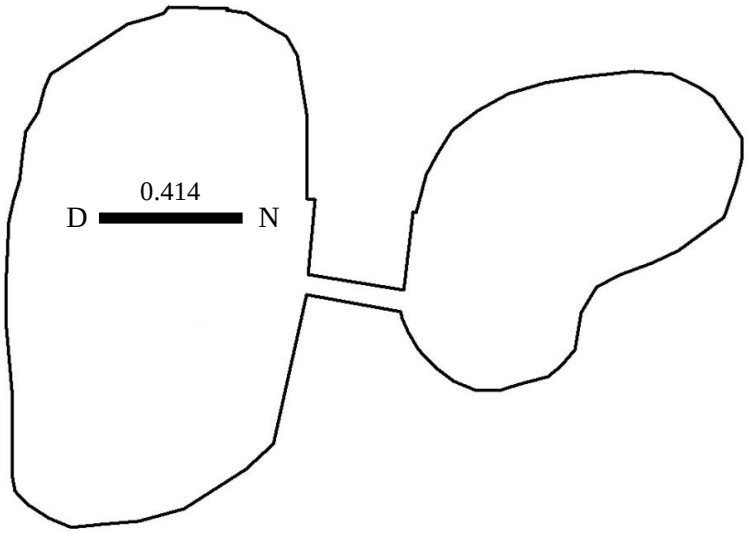

Figure 5.20. Corrected index of association for Dave and his sister Nina at Exmoor Zoo.

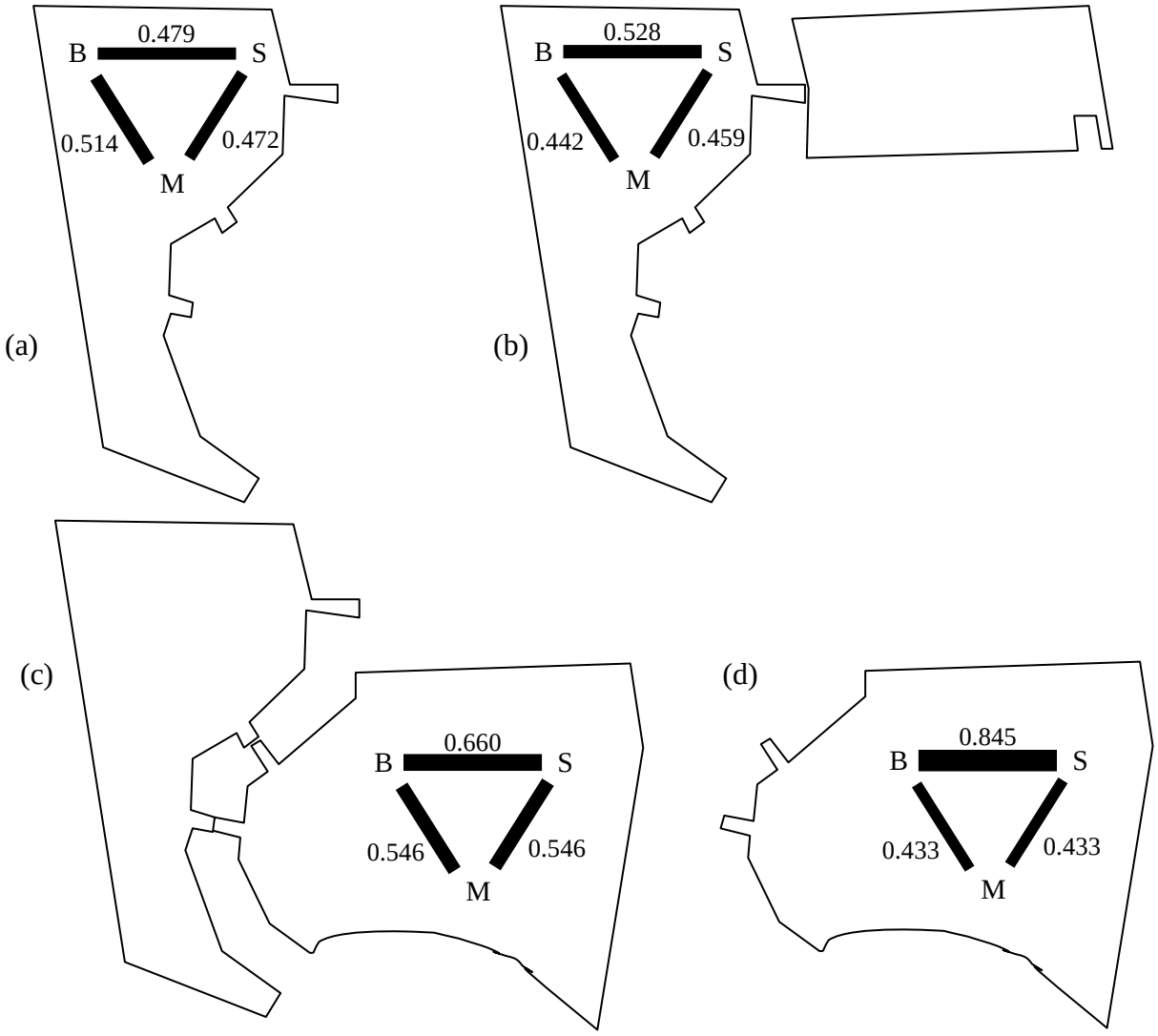

Figure 5.21. Corrected indices of association for related males Burba and Singa and unrelated male, Matrah in (a) Enclosure 1 only, (b) Enclosures 1 & 2, (c) Enclosures 1 & 3, (d) Enclosure 3 only at Chester Zoo.

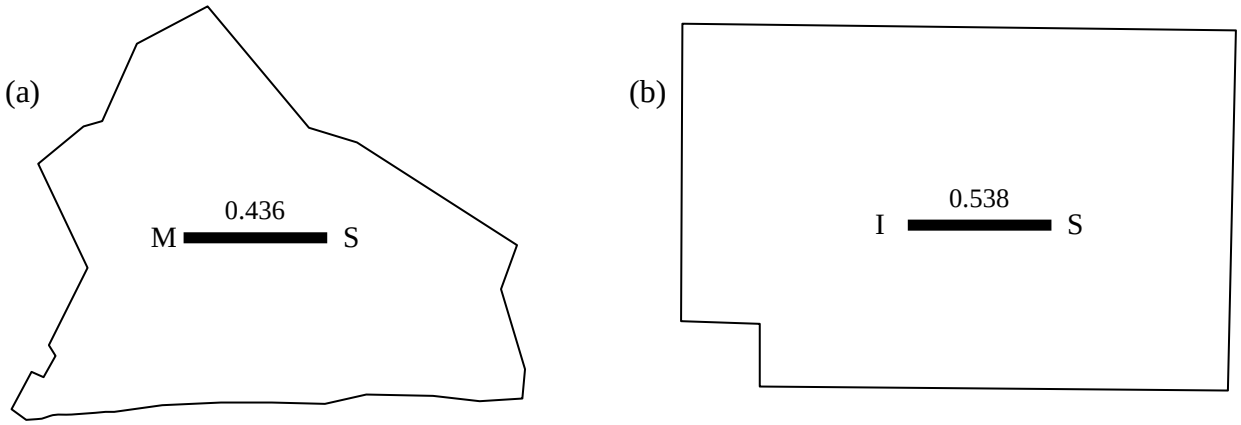

Figure 5.22. Corrected indices of association for (a) related males Moshi and Sifiso and (b) related females Izzy and Split at Port Lympne.

Figure 5.23. Corrected indices of association for related males Munya and Belika and unrelated males Cheetor and Duma at West Midland Safari Park.

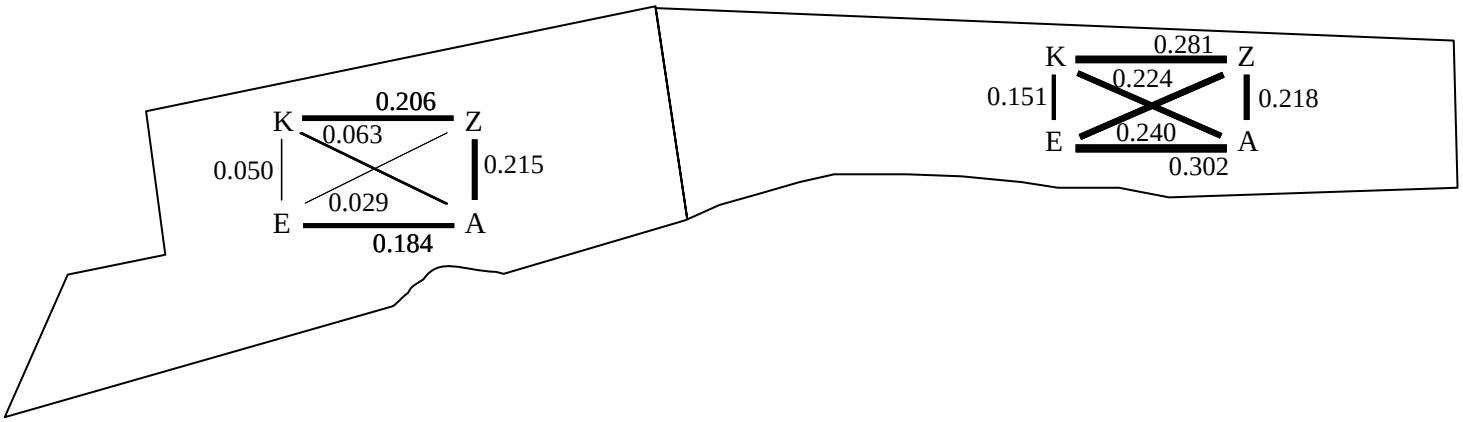

Figure 5.24. Corrected indices of association for related females Epesi and Azizi and unrelated females Kiwara and Zuri at West Midland Safari Park.

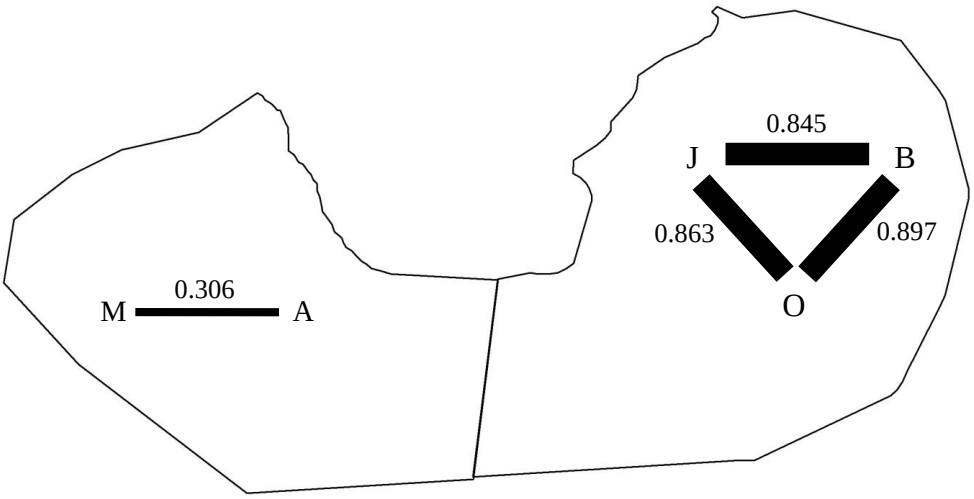

Figure 5.25. Corrected indices of association for unrelated males Maktoum and Al Safa, and related males Jake, Brooke and Oscar at ZSL Whipsnade Zoo.

Male-only dyads were more closely associated than female-only dyads ($U = 102.0$, $n_1 = 29$, $n_2 = 13$, $p<0.05$), and related individuals were more closely associated than unrelated individuals ($U = 71.0$, $n_1 = 14$, $n_2 = 29$, $p<0.01$). Related individuals were also more closely associated when male-only dyads and female-only dyads were analysed separately (Figure 5.26). This difference was significant for males but not for females (males: $U = 31.0$, $n_1 = 10$, $n_2 = 19$, $p<0.01$; females: $U = 6.0$, $n_1 = 3$, $n_2 = 10$, $p>0.05$).

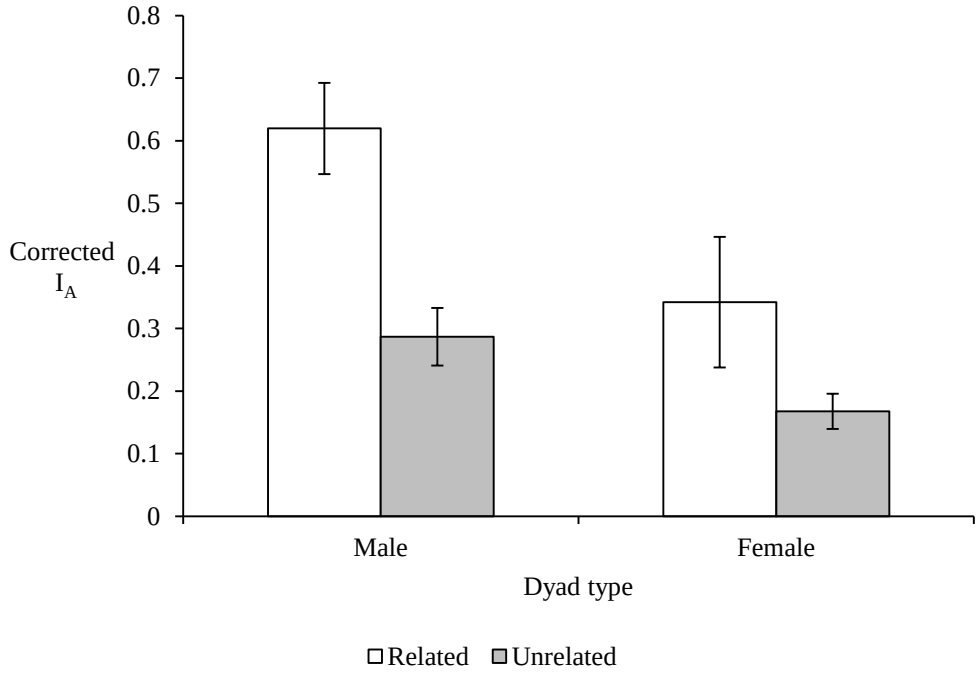

Figure 5.26. Corrected indices of association for related and unrelated male-only dyads and female-only dyads. Error bars represent the standard error of the mean.

Rates of allogrooming among all dyads were positively correlated with corrected indices of association (Spearman's rank-order correlation coefficient: r_s = 0.675, n = 43, p<0.001). There was no significant relationship between indices of association and rates of aggression (r_s = 0.128, n = 43, p>0.05). In male-only dyads, rates of allogrooming were positively correlated with corrected indices of association (Figure 5.27 (a); r_s = 0.594, n = 29, p = 0.001), and there was no significant relationship between indices of association and rates of aggression (Figure 5.27 (b); r_s = 0.273, n = 29, p>0.05).

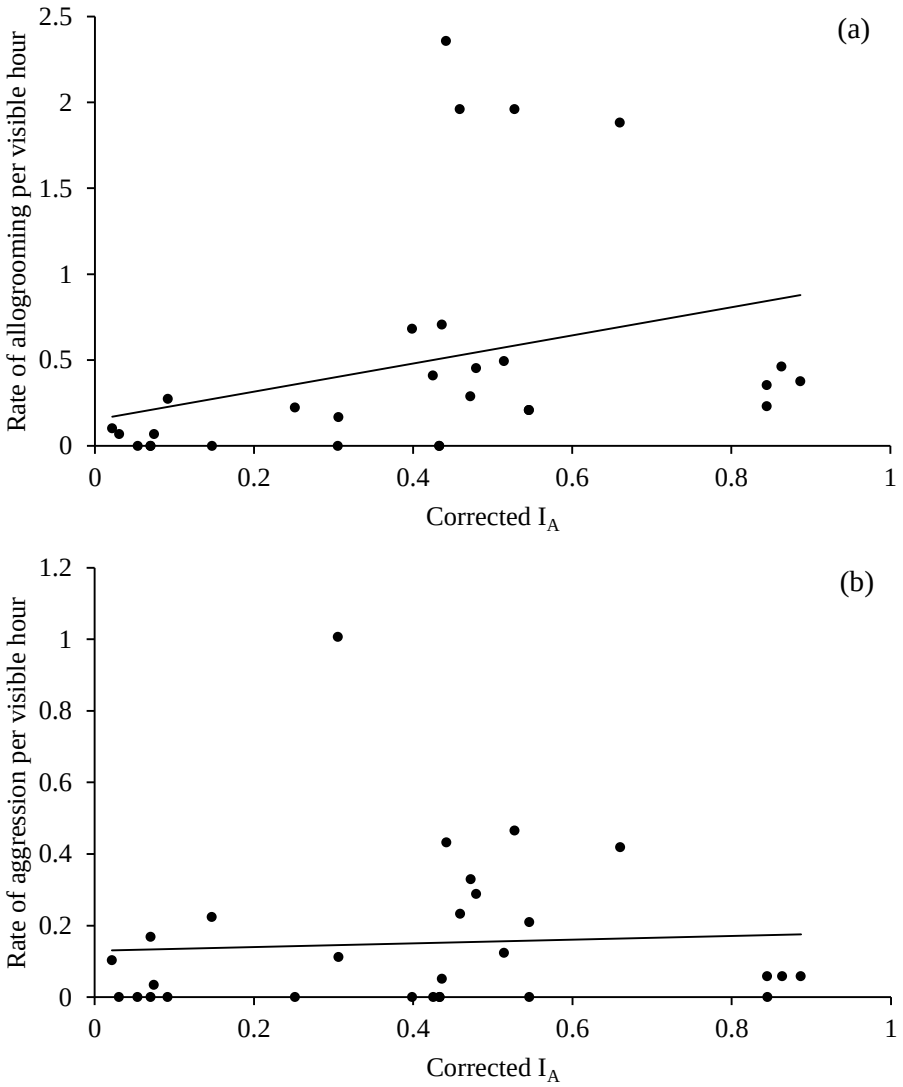

Figure 5.27. Relationship between corrected indices of association and rates of (a) allogrooming and (b) aggression among male-only dyads.

In female-only dyads, rates of allogrooming were positively correlated with indices of association (Figure 5.28 (a); r_s = 0.777, n = 13, p<0.01). There was a negative relationship between indices of association and rates of aggression among females; this relationship approached significance at the 5% level (Figure 5.28 (b); r_s = -0.514, n = 13, p = 0.072).

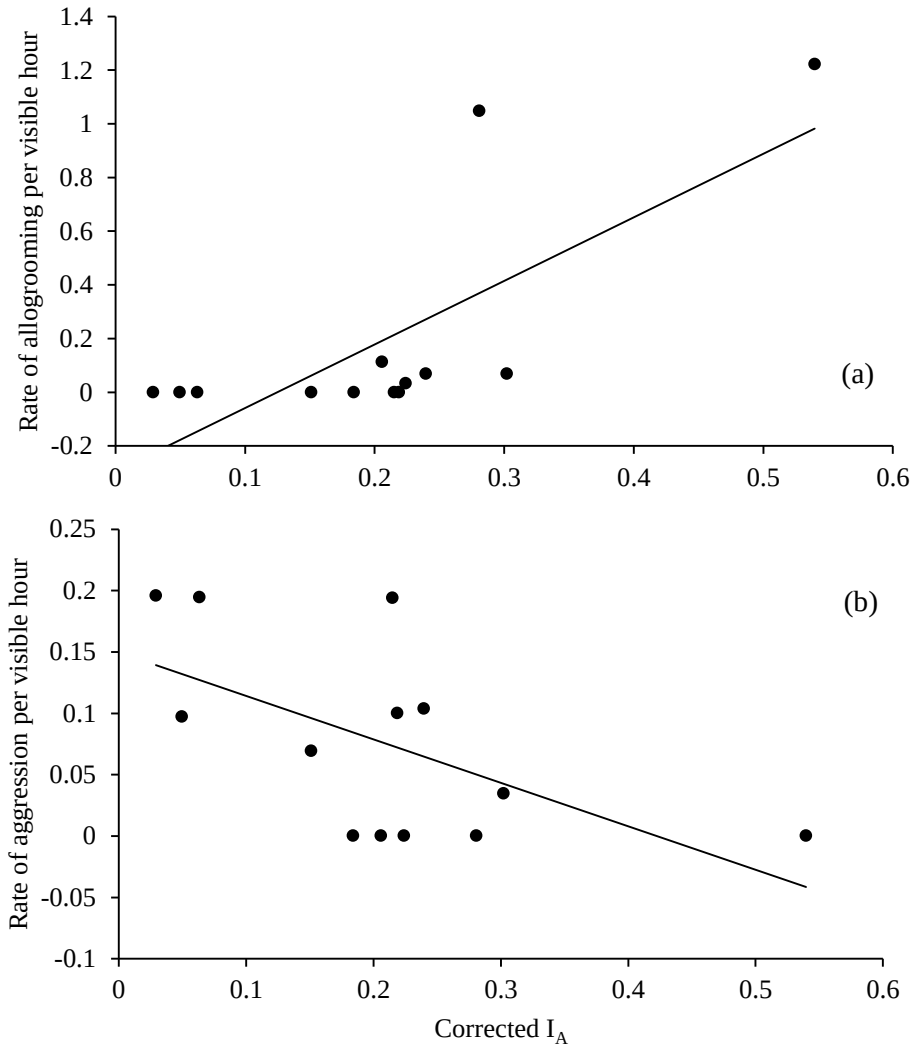

Figure 5.28. Relationship between corrected indices of association and rates of (a) allogrooming and (b) aggression among female-only dyads.

5.4. Discussion

The objective of the research presented in this chapter was to investigate spatial association in group-housed cheetahs. A new method was developed for determining the likely effect of chance encounters on indices of association, and for correcting observed association indices. Following previous research into the behaviour of coalitions in the wild (Caro, 1994), it was hypothesised that males housed in groups in captivity would maintain close proximity to one another and that related males would be more closely associated than

unrelated males. Spatial analyses revealed that indices of association were significantly higher for related males than unrelated males, and that affiliative interactions were positively correlated with indices of association. Results therefore support this hypothesis.

Additionally, due to their solitary nature in the wild, it was predicted that weak associations would be found among group housed females. Observed indices of association were higher than those calculated using chance encounters and no significant difference was found between association indices of related and unrelated females. Affiliative behaviours were also observed in some female-only dyads. Results therefore partly support this hypothesis, since in some cases females were closely associated and displayed affiliative behaviours, whilst in other cases they were seen in proximity without interacting with one another.

Studies using an association index to quantify social relationships should take into account chance encounters. There have been few attempts to estimate – and thus control for – the effects of chance encounters on indices of association. Here, a simple Monte Carlo simulation was devised to produce a new method of calculating the probability a of chance encounter when particular distance criteria for defining associations were used in shapes of a particular area. Results showed that when the distance criterion was set at 5 units, the probability of a chance encounter was negligible (less than 0.05) when the area was greater than 1500 units^2, and that the area's shape did not affect the probability of a chance encounter in areas larger than 50 units^2. As would be expected, increasing the distance criterion that defined association from 1 unit through 10 units resulted in an increase in the probability of a chance encounter. The simulation can be used to estimate the probability of chance encounters between individuals in any confined space. This includes studies of captive animals as well as wild or semi-wild populations, where home range sizes, natural habitat boundaries or the extent of overlap in the home ranges of individuals are known.

As area increased, the probability of a chance encounter decreased. Animals housed in larger enclosures or with large areas of home range or territory overlap are less likely to be observed in proximity simply by chance than those in smaller enclosures or with a lesser extent of overlap in their home ranges. High indices of association for dyads in large areas may therefore be considered to represent actual associations among individuals. However, associations can occur between animals in confined spaces for reasons other than the animals choosing to be together; for example mutual attraction to resources (e.g. food, prey, water or shelter), or, in captive animals, gathering at the entrance to indoor accommodation.

Passive associations occur when individuals independently converge on a mutual attraction, and have been observed in wild orang-utans (Mitani *et al*., 1991), male chimpanzees (Pepper *et al*., 1999), female spider monkeys (Ramos-Fernández *et al*., 2009) and female chacma baboons (*Papio hamadryas ursinus*: Henzi *et al*., 2009). In captivity, Stoinski *et al*. (2001) found that captive gorillas in four different exhibits spent significantly more time near to holding buildings than would be expected by chance. The authors proposed familiarity with the buildings, associations between the buildings and positive events such as feeding, and protection from environmental conditions as possible explanations for this preference. Captive felids also demonstrate preferences for specific areas of their enclosures, including edges and elevated areas (Lyons *et al*., 1997; Mallapur *et al*.. 2002). Indices of association should therefore be interpreted alongside behavioural observations of affiliative or aggressive interactions, since relationships are not solely based on spatial proximity (Whitehead, 2008a).

With the distance criterion set at 5 units, significant effects of shape on the probability of a chance encounter were only found when area was less than 50 units^2. In the circle measuring 20 units^2, the maximum distance between the random points was 4.999 units. Given that the diameter of this circle was 5.05 units and the distance criterion was set at 5

units, it was highly unlikely that individuals would be deemed not associating. In the square of the same area, the length of the diagonal was 6.33 units and the maximum distance between the random points was 6.23 units. Thus, it was more likely that two randomly generated points would be further than 5 units apart in the square than in the circle. Similarly, Stricklin *et al*. (1979) found that the shape of a pen affected the mean distance between nearest neighbours when pen size was held constant at 10,000 units^2, with greater distances between nearest neighbours in the square pen than in the circle.

Modern zoo exhibits are rarely constructed in regular, geometric shapes, so the effect of shape on the probability of chance encounters was further investigated by applying the simulation to spatially-referenced images of actual zoo enclosures. Significant differences in the probability of a chance encounter between actual zoo enclosures and squares of the same area were only found in the combinations of Enclosures 1, 2 and 3 at Chester Zoo and the enclosure at Exmoor Zoo. These were the enclosures that least resembled squares, yet the calculated effect sizes were small. The simulation can therefore be used to calculate chance encounters in irregular, non-geometric shapes.

As would be expected, increasing the distance criterion that defined association from 1 unit through 10 units resulted in an increase in the probability of a chance encounter. It is important for researchers to select a distance criterion that defines an association which is biologically relevant to their study species. In their review of techniques for analysing vertebrate social structure, Whitehead and Dufault (1999) found large variation in the distances between individuals which constituted an association. Some authors considered animals to be associated if they were within 1m of each other (e.g. captive common marmosets: Koenig & Rothe, 1991), and in other studies animals were considered to be associated if they were within 500m of each other (e.g. wild giraffes: Leuthold, 1979). The definition of an association will depend upon the interactions and behaviours of the study

species and the ease of observing individuals. Nonetheless, the results of the simulation highlight the importance of selecting an appropriate definition of association that corresponds to the behaviour of the animals being studied.

There were no significant differences in the probability of a chance encounter when random points were generated in square shapes using Microsoft® Excel and Geographic Information Systems. Given that significant effects of shape were only found when area was less than 50 units^2, the simulation devised in Microsoft® Excel is valid for predicting chance encounters in areas of different shapes. Thus, this simple simulation was used to produce a probability table for chance encounters within a dyad in areas ranging from 20 units^2 to 10,000 units^2, with distance criteria of between 1 and 25 units (Appendix 2). The table can be used by researchers as a guide to determine whether or not chance encounters are of concern.

The results of the simulation can also be used to correct observed indices of association (Chadwick *et al*., 2013), by calculating an index of association based on the simulated number of chance encounters and subtracting it from the index calculated using field observations. This correction is especially relevant when animals are limited to small spaces. Correcting the index in this way facilitates direct comparisons of association indices for dyads housed in enclosures of different sizes in multi-zoo studies, or for pairs with different sized territories (Chadwick *et al*., under review).

Indices of association, corrected using the results of the simulation, showed that related individuals were more closely associated than unrelated individuals. Furthermore, rates of allogrooming were positively correlated with indices of association in both male-only dyads and female-only dyads. Thus, individuals within closely associated dyads were not only seen in proximity, but also displayed affiliative behaviour. Among males, no significant correlation was found between rates of aggression and indices of association. The strength of relationship among males was therefore related to the strength of affiliation, rather than

agonistic behaviour. In contrast, a negative relationship emerged between aggression and association among females. The results also revealed gender differences in the effect of relatedness on indices of association. Within all-male groups, related males were significantly more closely associated than unrelated males, whilst no significant difference was found between association indices of related and unrelated females. In addition, interesting patterns of association also emerged within individual enclosures.

The behaviour and association patterns observed in the coalition of three males at Chester Zoo are particularly worthy of note because they mirror the formation of wild coalitions containing unrelated individuals. In the Serengeti, Caro (1994) observed three coalitions of three males, each consisting of two littermates and one non-littermate. He noted that the siblings in a newly formed coalition of three spent more time in closer proximity to one another than they did in proximity to their unrelated companion, but in a comparable coalition that had been established for four years, these differences were no longer apparent. Caro (1994) also observed that allogrooming between siblings in a trio was more frequent than allogrooming between a sibling and a non-sibling. In the present study, indices of association and allogrooming rates within the three dyads were similar.

Burba, Matrah and Singa had been group-housed at Chester Zoo for four years. Siblings Burba and Singa arrived together and Matrah, who is not related to either Burba or Singa, was introduced in 2008. At the time of the introduction, all three males were approximately 20 months old. Initially, the two siblings were more closely associated with each other than with their unrelated companion (Chadwick *et al*., 2013). Corrected indices of association calculated from observations carried out in May 2009, five months after the introduction, were 0.723 for Burba and Singa, and 0.440 and 0.406 for Burba and Matrah and Singa and Matrah, respectively (Chadwick *et al*., 2013). The present data, collected four years on, show that whilst Burba and Singa were still more closely associated with each other, they

were seen in proximity with Matrah more often than when he was first introduced (Figure 5.21). Furthermore, rates of allogrooming between the three dyads were similar (Burba and Singa: 0.94 occurrences/hr; Burba and Matrah: 1.25 occurrences/hr; Singa and Matrah: 0.89 occurrences/hr). Thus, Burba, Singa and Matrah can be described as an established coalition of three, consisting of two siblings and one unrelated male.

All-male groups consisting of siblings alone were housed at Port Lympne and ZSL Whipsnade Zoo. At Port Lympne, Moshi and Sifiso were frequently seen in proximity (Figure 5.22a). They were observed allogrooming on several occasions and only one aggressive interaction between them was recorded. At Whipsnade, indices of association between Jake, Brooke and Oscar were high (Figure 5.25) and they were never seen more than 37.3m away from one another, even though the area of the enclosure was 2,269m^2. This is to be expected, given that brothers in the wild remain together for life and maintain close proximity to one another (Caro, 1993, 1994). However, it should be noted that Jake, Brooke and Oscar were observed during only one visit in May 2012, when the mean daily temperature was 21°C. Due to the warm weather, their activity levels were low (see Sub-section 4.4.1 of Chapter 4 for a comparison of activity levels and temperature). This may have falsely inflated their index of association, as if they had been more active and moved around the exhibit more, the indices of association between them could potentially have been lower. However a repeat visit at a different time of year was not made to Whipsnade due to the constraints of the study. Nonetheless, the trio displayed evidence of attachment and rates of aggression among them were low.

At West Midland Safari Park, siblings Munya and Belika were housed with unrelated males Cheetor and Duma since 2008. Unlike the males at Chester Zoo, differences in the indices of association between related and unrelated dyads in this group were observed. Munya and Belika were more closely associated with one another than with unrelated

individuals (Figure 5.23). Interestingly, a closer association was also found between Cheetor and Duma (Figure 5.23). Even though all four members of this group were seen within 1m of each other on several occasions, it appears that two dyads formed stronger associations. Allogrooming was more frequent between Munya and Belika than any other dyad in this enclosure (0.49 occurrences/hr); however Cheetor and Duma also groomed each other often (0.34 occurrences/hr).

The only all-male group consisting of unrelated individuals alone was housed in the second enclosure at Whipsnade Zoo. Maktoum and Al Safa were housed together in a mixed-sex group in 2008, before being separated from the females and housed as a pair in 2009. The index of association calculated for this dyad was 0.306. Allogrooming was never observed in this dyad, and aggressive interactions were more frequent between them than any other dyad in the study (1.01 occurrences/hr). However, they were only observed more than 30m apart on 13 of 280 occasions, and the distance between them was less than 15m on 217 sample points. This dyad, it seems, used the same areas of the enclosure at the same time, without displaying any evidence of attachment. Similarly, Ruiz-Miranda *et al*. (1998) observed few affiliative interactions among non-sibling males, as well as lower vocalisation rates in a non-sibling pair than a sibling pair during separation trials. They suggested that length of time spent together might explain these observed differences between the affiliative behaviours of sibling and non-sibling coalitions. However in the present research, Maktoum and Al Safa had been pair housed for three years; a similar length of time as non-siblings Matrah and Burba and Matrah and Singa at Chester Zoo, who had been housed together for four years. Unrelated males in the Chester group displayed evidence of attachment, whilst Maktoum and Al Safa did not. It is possible that other factors, such as individual variation, affect the behaviour of unrelated dyads (Ruiz-Miranda *et al*., 1998).

Taken together with the results presented in Chapter 4, these findings provide quantitative evidence that natural social groupings of wild male cheetahs can be replicated in captivity. It is possible to house male cheetahs in coalitions in captivity with few aggressive interactions, and social group housing allows male cheetahs to exhibit the species-specific social behaviours that have been observed in their wild counterparts (Caro & Collins, 1986; Caro, 1993, 1994; Chadwick *et al*., 2013). Coalitions can be characterised by mutual tolerance, affiliative behaviour and the maintenance of close physical proximity (Olson & Blumstein, 2009), as also seen in bottlenose dolphins (Connor *et al*., 1992) and African lions (Schaller, 1972). The coalitions in this study not only maintained close proximity with one another, but were also frequently seen allogrooming.

The investigation of association patterns among captive female groups was particularly important, since this is an unnatural group type for this species. Related females were more closely associated than unrelated females; however this difference was not found to be significant. Location data on all-female groups were collected at Port Lympne and West Midland Safari Park. Siblings Izzy and Split at Port Lympne (Figure 5.22b) were closely associated and were also seen allogrooming (1.22 occurrences/hr). Aggression was never observed in this dyad. At West Midland Safari Park, Kiwara, Epesi, Zuri and Azizi were housed together since 2008. There appeared to be no preferred associations within this group even though Azizi and Epesi were siblings (Figure 5.24). Few instances of allogrooming were observed in this group, with the exception of Kiwara and Zuri (0.76 occurrences/hr). Thus, for the most part, the members of this group were not frequently seen in proximity and did not often interact when they were in proximity to one another. It therefore appears that this group of females were tolerant of one another, without forming particular social bonds.

The results of behavioural observations presented in Chapter 4 revealed that aggressive interactions among females were rare. Spatial analyses presented in this chapter

have shown that group housed females were observed in close proximity more often than simply by chance. This is despite the solitary nature of wild female cheetahs. In some cases, females were closely associated and displayed affiliative behaviours, whilst in other cases they were seen in proximity without interacting with one another. These findings highlight the importance of using behavioural observations alongside indices of association when investigating social relationships, since relationships are not solely based on spatial proximity (Whitehead & Dufault, 1999). Even though they were observed in proximity, rates of aggression between females ranged from zero to only 0.2 occurrences per hour. In addition, the negative relationship between rates of aggression and indices of association in females suggests that group-housed females were able to successfully avoid confrontation. These results confirm the notion that female cheetahs can be safely housed together in compatible groups. However, as discussed in Section 4.5 of Chapter 4, results of behavioural observations suggested that group housing of females should be avoided.

It is acknowledged that digitising cheetah locations in the GIS from recordings made in the field can introduce errors into the analysis. The analysis relied on the accuracy of the digitised points, which in turn required accurate location recordings in the field. It is possible that the locations of the cheetahs in the exhibit and the locations recorded onto the maps may have differed slightly, and it is not possible to retrospectively verify the recorded locations. This is a common problem in similar field studies using distance sampling techniques, where distances from transects to individual animals must be estimated. It has been established that observer experience improves the accuracy of distance sampling (Anderson *et al*., 2001; Lee & Marsden, 2008). In the present research, cheetah locations were recorded for 748 hours over a period of two years and the same technique was used for 124 hours of observation in a previous study (Chadwick *et al*., 2013). In addition, the fact that one observer conducted all

observations removed any possible effects of inter-observer variability (Martin & Bateson, 2007; Lee & Marsden, 2008).

One other option was to remotely collect location data using GPS units; however this was prevented by the need to anaesthetise the animals before GPS collars could be fitted. Invasive procedures such as this were not permitted by the participating zoos. In addition, this research used GIS on an unusually small scale; GIS techniques have previously been used for macro scale habitat selection and home range analysis. Given that the accuracy of commercially available GPS units can range from 3m to 30m (Frair *et al*., 2010), GPS collars would not have been adequate to collect the location data required for this research. It is also possible that the accuracy of GPS equipment could have varied between sites due to the locations of trees and buildings within and around the exhibits (see Section 3.4 of Chapter 3 for a discussion of the limitations of GPS).

Whilst efforts were made to correct the observed association indices to take into account chance encounters, the methods used to estimate chance encounters were subject to three assumptions. Both methods of random point generation assumed that resources were evenly distributed throughout the area; that animals made use of the whole area and that each consecutive location plotted for each individual in the dyad was independent of the previous location. This was not the case in the field study, where it was possible that mutual attraction to resources, such as the small shelters in the enclosures, influenced the resulting association indices. Despite this, the use of observations of social interactions alongside spatial associations allows conclusions to be drawn about the social relationships between individuals in the same enclosure.

5.5. Conclusion

Studies using an association index to quantify social relationships should take into account chance encounters, since animals may be observed in proximity for reasons other than attempting to associate. Research presented in this chapter outlined a new method for correcting indices of association, using the results of a simple Monte Carlo simulation. This facilitated the comparison of association indices for dyads housed in different sized enclosures. Corrected indices of association revealed that male-only dyads were more closely associated than female-only dyads. Within male-only dyads, related individuals were more closely associated than unrelated individuals. However, this difference was not apparent among females. These association patterns would be expected, given the social nature of wild males and the solitary nature of wild females. In addition, indices of association should not be used in isolation to describe social relationships. Rates of allogrooming were positively correlated with indices of association in the present research. Thus, individuals within closely associated dyads were not only seen in proximity, but also displayed affiliative behaviour.

Spatial analyses presented in this chapter have reiterated the findings presented in Chapter 4 and provided more detailed information about social and spatial relationships among group housed cheetahs. Successful management of captive animals, however, depends not only on the management of populations or groups, but also on the management and husbandry of individual animals. The following chapter investigates the effects of individual variation in personality on behaviour, social group cohesion and reproductive success.

6. Personality, social group cohesion and reproductive success in captive cheetahs

6.1. Introduction

6.1.1. Background

Results presented in Chapters 4 and 5 provided the first evidence of the effects of social group housing on cheetah behaviour, and new information on social behaviour and association within captive cheetah groups. The success of captive breeding programmes, however, depends not only on the management of populations or groups, but also on the management and husbandry of individual animals. The captive environment has a profound effect on the behaviour of wild animals (Hosey, 2005; Morgan & Tromborg, 2007) and individuals vary in their responses to environmental variables. Understanding this variation among individuals is the goal of animal personality research.

Recently, several authors advocated the assessment of animal welfare from the perspective of the individual, rather than the species or taxon (Hill & Broom, 2009; Whitham & Wielebnowski, 2009, 2013; Watters & Powell, 2012). Indeed, research by King, Weiss and colleagues (Weiss *et al*., 2002; King & Landau, 2003; Weiss *et al*., 2006, 2009) has provided evidence that welfare is related to personality in great apes. Personality has been linked to other, more established indicators of welfare, such as stereotypic behaviour (Ijichi *et al*., 2013; Shepherdson *et al*., 2013) and levels of stress hormones (Wielebnowski, Fletchall *et al*., 2002; Grand *et al*., 2012; DeCaluwe *et al*., 2013; Shepherdson *et al*., 2013). Knowledge of animal personality has the potential to inform important decisions relevant to breeding and welfare, and research into zoo animal personality has provided insights into the reproductive failure of individuals, the compatibility of breeding pairs and the stability of social groups (Tetley & O'Hara, 2012).

One focus of recent research into zoo animal personality has been the effect of personality on individual breeding success. The literature in this area is dominated by studies on those species that display poor reproductive success in captivity (Carlstead, Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999; Wielebnowski, 1999; McKay, 2003; Powell *et al*., 2008; Baker & Pullen, 2013; DeCaluwe *et al*., 2013), which might indicate underlying welfare concerns. In particular, a relationship has emerged between fearfulness or shyness and reproductive success, as more fearful individuals are less likely to breed successfully (Wielebnowski, 1999; Powell *et al*., 2008; Smith & Blumstein, 2008).

If personality affects the reproductive success of individuals, it follows that the combination of personalities within a pair may predict the success, or failure, of that pair to reproduce. Behavioural incompatibility is often cited for the failure of a pair to successfully produce offspring (Snyder *et al*., 1996; Carlstead, Mellen *et al*., 1999; Augustus *et al*., 2006; McDougall *et al*., 2006; Freeman *et al*., 2009; Lees & Wilcken, 2009). Links between the personality profiles of individuals in successful and unsuccessful breeding pairs have been uncovered in birds (Both *et al*., 2005; Spoon *et al*., 2006; Schuett *et al*., 2010, 2011) and black rhinoceros (Carlstead, Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999). However, little is currently known about the potential effects of personality combinations on the reproductive success of zoo mammals, despite the findings of Carlstead and her colleagues (Carlstead, Fraser *et al*., 1999; Carlstead, Mellen *et al*., 1999) that personality is a good predictor of pair compatibility.

There is evidence that the personalities of individuals within a social group can affect the social compatibility, stability, relationships and success of that group (Hessing *et al*., 1994; Murray, 1998; Kuhar *et al*., 2006; Watters & Meehan, 2007; Miller & Kuhar, 2008; Freeman *et al*., 2010b; Massen & Koski, 2014). For example, male gorillas scoring highly on an ‘understanding’ personality factor were more likely to be successfully housed in social

groups and displayed high rates of affiliative behaviour (Kuhar *et al*., 2006). Similarly, chimpanzee friendships, characterised by time spent sitting in contact, were related to small absolute differences between individuals in sociability and boldness (Massen & Koski, 2014).

Personality has been assessed in five species of captive felids, including cheetahs (Wielebnowski, 1999; McKay, 2003; Baker & Pullen, 2013), clouded leopards (Wielebnowski, Fletchall *et al*., 2002; DeCaluwe *et al*., 2013), Scottish wildcats (Gartner & Weiss, 2013b), snow leopards (Gartner & Powell, 2012) and tigers (Phillips & Peck, 2007), as well as the domestic cat (Feaver *et al*., 1986). All of these studies adopted a trait rating method, and the results showed that keepers are able to reliably rate felid personality traits. Most studies validated trait ratings with observations of behaviour and biological measurements. Wielebnowski (1999) found that cheetahs rated as more aggressive by their keepers were more likely to hiss, growl and stare at their mirror image. Similarly, DeCaluwe *et al*. (2013) observed more hiding behaviour and elevated faecal glucocorticoid metabolite levels in clouded leopards rated as anxious.

This research is the first of its kind to investigate cheetah personality in the EEP region; previous studies have focused on cheetahs housed in zoos in either the UK (McKay, 2003; Baker & Pullen, 2013) or USA (Wielebnowski, 1999) only. Wielebnowski (1999) uncovered a link between cheetah personality and individual breeding success. She found that cheetahs that had bred successfully were rated as less tense and fearful by their keepers than cheetahs that had not bred successfully. However, a study by McKay (2003) failed to find a link between personality and breeding success. This may have been due to the small number of breeding individuals within the sample; only seven of 41 cheetahs had bred successfully (McKay, 2003). In a more recent study, Baker and Pullen (2013) attempted to correlate cheetah personality with husbandry variables. They found that dominance scores were lower if cheetah keepers routinely entered the enclosure with the animals, and speculated that these

individuals were less fearful because they had regular contact with their keepers. They also found that males scored higher than females on a sociability component, which may relate to the natural social tendencies of both sexes. However, there was little variation in the social groups maintained in that study, with only group-housed males and singly-housed females included in the sample.

Given that cheetah personality can be reliably rated by keepers (Wielebnowski, 1999; McKay, 2003; Baker & Pullen, 2013) and that these ratings are valid and related to behaviour (Wielebnowski, 1999), the assessment of personality may prove to be a valuable tool for captive cheetah care providers. However, despite the findings of previous studies, little further research has been published into the effects of personality on the behaviour and reproductive success of captive cheetahs.

6.1.2. Objective and hypothesis

This chapter aims to address Objective 3 of the research:

- *To explore the relationship between cheetah personality profiles, behaviour and breeding success.*

Previous research has suggested that personality may be correlated with breeding success (Wielebnowski, 1999), and that the individual personalities in a breeding pair or social group might influence the success of that pair or group (Murray, 1998; Carlstead, Mellen *et al*., 1999; Kuhar *et al*., 2006). Thus, information about the personality of an individual could be invaluable to staff at institutions involved in co-ordinated captive breeding programmes. It is hypothesised that keepers will be able to reliably rate cheetah personality, and that their ratings are valid and related to behaviour (Wielebnowski, 1999; McKay, 2003; Baker & Pullen, 2013). Further, it is predicted that individuals that have bred successfully will be rated as less fearful by their keepers than those that have not bred successfully (Wielebnowski,

1999), and that individuals housed in social groups will score highly on personality traits related to sociability (Murray, 1998; Kuhar *et al*., 2006). In addition, this research will investigate pair compatibility in cheetahs by comparing the personality profiles of successful and unsuccessful breeding pairs.

Objective 3 is investigated using a cheetah personality questionnaire, completed by cheetah keepers at 31 zoos. The keepers' responses were examined for reliability and compared with direct behavioural observations of a sub-sample of 32 cheetahs. Principal Components Analysis was used to reduce the data set into six components of cheetah personality, which were examined in relation to social group housing, reproductive success, gender and rearing history.

6.1.3. Outline of the chapter

A review of the literature relevant to this chapter is presented in Chapter 2. A review of studies of animal personality is presented and the applications of personality assessment to the management and welfare of zoo mammals are discussed in Section 2.7. Results of previous studies of felid personality are reviewed in Section 2.8. A critical appraisal of the methods available for assessing zoo animal personality is presented in Section 3.5 of Chapter 3, where a justification for the methods adopted in this research is also provided.

Section 6.2 of this chapter describes the detailed procedures followed for the collection and analysis of personality data. Section 6.3 presents the results, divided into Sub-section 6.3.1 on keeper ratings, Sub-section 6.3.2 on the results of exploratory factor analysis and Sub-section 6.3.3 on personality scores in relation to breeding success, social group housing and rearing history. Finally, Section 6.4 discusses the findings of the cheetah personality survey, the implications of these findings for captive cheetah management and the limitations of the methodological approach.

6.2. Procedures

6.2.1. Subjects and participating zoos

Personality ratings were collected for 95 cheetahs in the EEP region (58 males and 37 females; Table 6.1) living in 27 zoos, representing 25% of the EEP cheetah population at the end of 2011. Keepers at the zoos visited for behavioural observations (Chapter 4) were asked to complete the cheetah personality questionnaire during one of the visits made for behavioural data collection. In addition, the questionnaire was distributed to a further two UK zoos (Colchester Zoo, Essex; Dartmoor Zoological Park, Devon) and 14 zoos across Europe participating in the cheetah EEP (Table 6.1). Cheetah Outreach (South Africa), Monarto Zoo (Australia), the National Zoo and Aquarium (Australia), and Wellington Zoo (New Zealand) also provided ratings for their animals. Ratings were received for 120 cheetahs in total (73 males and 47 females; Table 6.1), living in 31 zoos.

Initial contact was made by e-mail with the zoos that were not visited for behavioural observations. In the first instance, those zoos that were interested in participating in the research were asked to provide ARKS (Animal Record Keeping System) reports for their cheetahs. These reports detailed the names, ages, rearing history and studbook numbers of individuals. Each questionnaire was modified to include the names of the cheetahs and forwarded to the zoo by post or e-mail. At least two keepers from each participating zoo were asked to complete the questionnaire independently, without conferring.

Table 6.1. Subjects for which completed personality questionnaires were received from 31 zoos. Bold type denotes a zoo visited for behavioural observations.

Zoo	Country	Number of cheetahs (males.females)
EEP Participants		
Africa Alive!	UK	2.1
Banham Zoo	UK	0.1
Boras Djurpark	Sweden	5.2
Burger's Zoo	Netherlands	0.2
Chester Zoo	UK	3.2
Colchester Zoo	UK	2.3
Cologne Zoo	Germany	4.0
Dartmoor Zoological Park	UK	0.1
Dresden Zoo	Germany	2.0
Exmoor Zoo	UK	1.1
Marwell Wildlife	UK	1.2
Olmense Zoo	Belgium	1.0
Opel Zoo	Germany	1.1
Paignton Zoo	UK	1.1
Paradise Wildlife Park	UK	0.2
Peaugres Safari Park	France	8.5
Pilsen Zoo	Czech Republic	2.0
Port Lympne	UK	2.2
Silesian Zoo	Poland	4.2
Szeged Zoo	Hungary	4.0
Thuringer Zoo	Germany	2.0
Warsaw Zoo	Poland	2.1
West Midland Safari Park	UK	4.4
Wildlife Heritage Foundation	UK	1.0
Zagreb Zoo	Croatia	1.0
Zoo Landau	Germany	2.1
ZSL Whipsnade Zoo	UK	3.3
Non-EEP Participants		
Cheetah Outreach	South Africa	8.1
Monarto Zoo	Australia	5.6
National Zoo & Aquarium	Australia	0.3
Wellington Zoo	New Zealand	2.0

6.2.2. Keeper questionnaire

An adapted version of the questionnaire devised by Wielebnowski (1999) was used. Her questionnaire was found to have high inter-rater reliability and was validated by a mirror-image stimulation test. The questionnaire (Appendix 3) consisted of a form with between one and thirteen 120mm long horizontal lines, relating to the number of cheetahs at each zoo, for

20 behavioural characteristics (Table 6.2). Cheetah keepers were asked to rate each animal based on their own knowledge and general impression of the individual's behaviour, and to indicate their rating by placing a cross on the line. The distance from the left of the line to the cross was then measured in millimetres, providing a numerical score for each animal of between 0 and 120 and allowing traits to be rated on a continuous scale (Feaver *et al*., 1986; Wielebnowski, 1999; Martin & Bateson, 2007).

The original questionnaire consisted of 18 personality traits (Wielebnowski, 1999). Since animals may behave differently in the presence of their keepers and people with whom they have no regular contact (Mitchell *et al*., 1991; Hosey, 2008), it was decided to split the two traits 'aggressive to people' and 'fearful of people', from the original questionnaire, into four: 'aggressive to familiar people'; 'aggressive to unfamiliar people'; 'fearful of familiar people' and 'fearful of unfamiliar people' (Table 6.2).

In addition, keepers were asked to provide some information about themselves, including how long they had worked with cheetahs, how long they had worked with animals in general and how much time they spent per week with the current group of cheetahs. Keepers were also asked whether or not they believed there were distinct personalities among their cheetahs, and if they thought that personality could be correlated with reproductive success, disease, or how an individual copes with stress. Comment sheets were provided at the end of the questionnaire, on which keepers were encouraged to add any further adjectives that they felt described the behaviour of the cheetahs.

Table 6.2. Behavioural definitions of 20 cheetah personality traits. Adapted from Wielebnowski (1999).

Trait	Definition
Active	Moves around enclosure (e.g. paces, runs, stalks)
Aggressive to conspecifics	Reacts hostile (e.g. attacks, growls) towards other cheetahs
Aggressive to familiar people	Reacts hostile and threatening to familiar keepers and staff members
Aggressive to unfamiliar people	Reacts hostile and threatening towards unfamiliar staff and members of the public
Calm	Not easily disturbed by changes in the environment
Curious	Approaches and explores changes in the environment
Eccentric	Shows stereotypic or unusual behaviours
Excitable	Overreacts to changes in the environment
Friendly to conspecifics	Initiates and seems to seek proximity of other cheetahs
Friendly to keepers	Initiates proximity with keepers: approaches fence readily and in a friendly manner (e.g. purrs, rubs on fence)
Fearful of conspecifics	Retreats and hides from other cheetahs
Fearful of familiar people	Retreats and hides from familiar keepers and staff members
Fearful of unfamiliar people	Retreats and hides from unfamiliar staff and members of the public
Insecure	Seems scared easily; "jumpy" and fearful in general
Playful	Initiates and engages in play behaviour (seemingly meaningless, non-aggressive behaviour) with objects and/or other cheetahs
Self-assured	Moves in a seemingly confident, well co-ordinated and relaxed manner
Smart	Learns quickly to associate certain events and appears to remember for a long time
Solitary	Spends time alone; avoids company
Tense	Shows restraint in movement and posture
Vocal	Frequently and readily vocalises

In order for the information provided by a personality study to be useful, the assessment of personality must be both reliable and valid (Gosling, 2001; Gosling & Vazire, 2002; Kuhar *et al*., 2006; Meagher, 2009; Freeman & Gosling, 2010). Raters scoring the animals must agree in their assessments or observations. This can be confirmed by testing inter-rater (or inter-observer) reliability (Gosling, 2001; Gosling & Vazire, 2002; Martin & Bateson, 2007; Meagher, 2009). Thus, the ratings obtained using the questionnaire were tested for reliability using Kendall's coefficient of concordance where three or more keepers provided ratings and Spearman's rank correlation coefficient where two keepers provided

ratings (Wielebnowski, 1999; Martin & Bateson, 2007; DeCaluwe *et al*., 2013). Reliability was assessed per trait, per zoo (Wielebnowski, 1999; Pankhurst *et al*., 2009).

The validity of the ratings was examined by comparing a sample of the survey results with the results of direct behavioural observations using Spearman's rank-order correlation coefficient (Wielebnowski, 1999; Kuhar *et al*., 2006; Freeman *et al*., 2010a; DeCaluwe *et al*., 2013). Keeper ratings were received for 32 of the 37 cheetahs on which behavioural observations had also been conducted (Joshi at Africa Alive! died and Nescio at Port Lympne was moved prior to ratings being collected, and Jake, Brooke and Oscar at ZSL Whipsnade Zoo were too young to be easily distinguished from their littermates at the time of rating). The percentage of visible time each individual spent performing each behaviour on the ethogram (Chapter 4) was correlated with their ratings on the 20 traits on the personality questionnaire. For infrequent behaviours or those of short duration, rates of behaviour per visible hour (Chapter 4) were correlated with the personality traits.

6.2.3. Principal Components Analysis

The mean rating on each trait for each cheetah was input into a Principal Components Analysis (PCA). PCA is a form of exploratory factor analysis and is an established technique for analysing the results of personality questionnaires (King & Figueredo, 1997; Carlstead, Mellen *et al*., 1999; Wielebnowski, 1999; Weiss *et al*., 2006, 2009; Pankhurst *et al*., 2009; Gartner & Weiss, 2013b). PCA reduces the data set into fewer, uncorrelated variables that represent most of the information obtained from the original variables (Wielebnowski, 1999; Tabachnick & Fidell, 2013). This means that, in personality studies, correlated traits are grouped into components. The resulting components are often referred to as personality dimensions.

In the present research, a PCA was conducted based on a Pearson's product-moment correlation matrix (Wielebnowski, 1999) with varimax rotation (King & Figueredo, 1997; Weiss *et al*., 2009; Field, 2013). Components with eigenvalues greater than 1 were retained (Wielebnowski, 1999; Field, 2013) and labelled according to the trait(s) that showed the highest positive loading(s) on the component (Wielebnowski, 1999). Absolute factor loadings ≥ 0.4 were considered salient (Weiss *et al*., 2006; Baker & Pullen, 2013; Gartner & Weiss, 2013b).

Standardised ratings (z-scores) were calculated for each cheetah for each trait (Equation 6.1: Gosling & Bonnenburg, 1998; Murray, 1998; Wielebnowski, 1999) and used to calculate component scores for each individual (Equation 6.2: Murray, 1998; Wielebnowski, 1999).

$$\text{Standardised rating } (z) = \frac{\text{individual's mean rating} - \text{sample mean}}{\text{sample standard deviation}} \qquad \text{Equation 6.1}$$

$$\text{Component score} = \sum \frac{\text{standardised rating on trait} \times \text{trait loading}}{\text{eigenvalue of component}} \qquad \text{Equation 6.2}$$

Component scores of individuals were subsequently compared to gender, breeding status (breeder or non-breeder), social group type (singly-housed or group-housed, where known) and rearing history (hand or parent reared) using Mann-Whitney U tests. Breeding status was defined as having sired (breeder) or failed to sire offspring (non-breeder). Individuals younger than 2 years of age, or those who had never been placed with a member of the opposite sex, were excluded from the comparison of component scores with breeding status. Mean absolute differences in the component scores of successful and unsuccessful

breeding pairs were also examined using Mann-Whitney U tests. A breeding pair was considered successful if they had produced at least one cub, surviving or not.

6.3. Results

6.3.1. Keeper ratings

In total, 97 keepers responded to the questionnaire. Keepers had worked with cheetahs for a mean of 6.9 years (σ = 6.89 years), and with animals in general for a mean of 13.2 years (σ = 9.52 years). The mean amount of time keepers spent working with the cheetahs was 5.8 hours per week (σ = 5.61 h). Almost all of the keepers who responded (98.9%) reported that they believed there were distinct personalities among their cheetahs, and 95% of keepers agreed with the statement that personality could be correlated with reproductive success, disease and how an individual copes with stress.

Cheetahs were rated by between one and nine keepers and the mean number of raters per cheetah was 2.86. Kendall's coefficient of concordance (*W*) was used to examine inter-rater reliability at 15 zoos where three or more keepers provided ratings. Mean values of *W* ranged from 0.51 for the trait aggressive to familiar people to 0.83 for the trait fearful of unfamiliar people, with an overall mean value of *W* of 0.69 (Table 6.3). Spearman's rank-order correlation coefficient (r_s) was used to examine inter-rater reliability at four zoos where two keepers provided ratings. Values of r_s varied from 0.37 for the trait eccentric to 0.87 for the trait vocal, with an overall mean value of r_s of 0.62 (Table 6.3). Due to the small numbers of cheetahs housed at the zoos (between two and 13), tests for inter-rater reliability did not always reach statistical significance. However, since the mean values of *W* were greater than 0.5 for all traits (Wielebnowski, 1999), and the overall mean values of both *W* and r_s were greater than 0.6 (Table 6.3), it was concluded that general reliability was good and all 20 traits were included in the PCA (Pankhurst *et al*., 2009).

At zoos where cheetahs were rated by only one keeper, or where two keepers had reached agreement and only provided one set of ratings, it was not possible to statistically assess reliability. However, animals for whom only one set of ratings were received were still included in the overall analyses, because inter-rater reliability for those animals rated by more than one keeper was found to be acceptable (Table 6.3; Dutton, 2008; Tetley & O'Hara, 2012).

Table 6.3. Mean values of Kendall's coefficient of concordance (three or more raters) and Spearman's rank-order correlation coefficient (two raters) for 20 personality traits.

Trait	Kendall's coefficient of concordance (*W*)	Spearman's rank-order correlation coefficient (r_s)
Active	0.65	0.82
Aggressive to conspecifics	0.55	0.70
Aggressive to familiar people	0.51	0.46
Aggressive to unfamiliar people	0.72	0.80
Calm	0.81	0.50
Curious	0.68	0.60
Eccentric	0.71	0.37
Excitable	0.77	0.77
Friendly to conspecifics	0.61	0.54
Friendly to keepers	0.68	0.81
Fearful of conspecifics	0.77	0.53
Fearful of familiar people	0.81	0.48
Fearful of unfamiliar people	0.83	0.51
Insecure	0.71	0.67
Playful	0.64	0.43
Self-assured	0.69	0.63
Smart	0.78	0.60
Solitary	0.65	0.57
Tense	0.65	0.64
Vocal	0.55	0.87
Overall mean	**0.69**	**0.62**

In the sub-sample of 32 individuals for whom both keeper ratings and behavioural observations were collected, significant correlations were found between trait ratings and direct observations of behaviour. Rates of aggressive behaviour (growling, hissing, slapping or biting directed at another) were positively correlated with the trait aggressive to

conspecifics (r_s = 0.427, n = 24, p<0.05), whereas rates of allogrooming (licking the fur of another) were negatively correlated with this trait (r_s = -0.570, n = 24, p<0.01). Aggressive behaviour was also positively correlated with the trait aggressive to unfamiliar people (r_s = 0.516, n = 24, p = 0.01). The percentage of visible time spent pacing (walking repeatedly along a definite path, e.g. along the fence of the exhibit) was positively correlated with the trait eccentric (r_s = 0.441, n = 32, p<0.05). Sniffing behaviour (crouching on forelegs with back legs supporting the body, inhaling through the nose) was positively correlated with the trait curious (r_s = 0.656, n = 32, p<0.001). There was a positive correlation between play behaviour (engaging in playful activities [seemingly meaningless, but non-aggressive behaviour] alone) and the trait playful (r_s = 0.538, n = 32, p = 0.001). Similarly, rates of social play (engaging in playful activities [seemingly meaningless, but non-aggressive behaviour] with another) were positively correlated with the trait friendly to conspecifics (r_s = 0.509, n = 24, p<0.05) and negatively correlated with the trait fearful of conspecifics (r_s = -0.538, p<0.01) and solitary (r_s = -0.527, n = 24, p<0.01).

6.3.2. Principal Components Analysis

PCA resulted in six components with eigenvalues greater than 1, which accounted for 67% of the total variance. The loadings of each trait onto the six components are presented in Table 6.4.

Table 6.4. Six major components of cheetah personality derived from ratings of 120 cheetahs at 31 zoos. Bold values indicate salient component loadings ≥ 0.4.

	Component[a]					
Trait	1	2	3	4	5	6
Active	-0.086	**0.716**	-0.124	0.270	0.248	0.059
Aggressive to conspecifics	-0.025	**0.440**	**-0.472**	-0.074	-0.117	**0.543**
Aggressive to familiar people	0.128	0.032	**-0.861**	-0.094	-0.049	0.140
Aggressive to unfamiliar people	0.630	0.305	-0.317	-0.008	-0.054	-0.225
Calm	-0.480	-0.173	0.120	-0.043	**-0.449**	-0.393
Curious	0.193	**0.693**	0.165	0.215	-0.285	-0.092
Eccentric	0.085	0.172	0.243	-0.099	**0.701**	-0.172
Excitable	0.076	-0.153	-0.062	0.128	**0.789**	-0.043
Friendly to conspecifics	0.095	0.025	0.290	**0.613**	-0.025	-0.236
Friendly to keepers	-0.175	0.283	**0.817**	0.140	0.004	0.169
Fearful of conspecifics	0.159	-0.166	0.065	-0.102	-0.162	**0.815**
Fearful of familiar people	**0.748**	0.063	-0.213	0.058	0.036	-0.047
Fearful of unfamiliar people	**0.795**	0.149	0.117	0.060	-0.150	0.003
Insecure	**0.752**	-0.214	-0.017	0.222	0.187	0.114
Playful	0.040	0.397	0.330	**0.676**	-0.076	0.293
Self-assured	**-0.613**	0.211	-0.013	0.078	-0.226	-0.174
Smart	-0.204	**0.529**	0.024	-0.030	**-0.434**	0.139
Solitary	-0.008	0.016	0.083	**-0.859**	-0.115	0.051
Tense	**0.596**	-0.144	-0.101	-0.312	0.281	0.244
Vocal	0.047	**0.561**	0.204	-0.237	0.117	-0.228
Eigenvalue	3.795	2.889	2.314	1.521	1.438	1.334
% of variance	18.98	14.50	11.57	7.61	7.19	6.67

[a]Component labels: 1: Fearful-insecure; 2: Active; 3: Friendly to keepers; 4: Friendly to conspecifics; 5: Excitable; 6: Fearful of conspecifics.

Component 1 was labelled ‘fearful-insecure’ and had high positive loadings on the traits fearful of unfamiliar people, insecure, fearful of familiar people, aggressive to unfamiliar people and tense. This component had high negative loadings on the traits self-assured and calm. Cheetahs scoring highly on this component were considered to be more fearful and tense, and less calm and self-assured than individuals with low scores. Component 2 had high positive loadings on the traits active, curious, vocal and smart, and was labelled ‘active’. Component 3, labelled ‘friendly to keepers’ had a high positive loading on the trait friendly to keepers and a high negative loading on aggressive to familiar people. Component 4 was labelled ‘friendly to conspecifics’ and showed high positive loadings on the traits friendly to

conspecifics and playful, with a high negative loading on the trait solitary. Component 5, labelled 'excitable', had high positive loadings on the traits excitable and eccentric. The trait calm was negatively loaded onto this component, meaning that cheetahs scoring highly on it were less calm and more likely to overreact to changes in the environment than cheetahs with low scores for this component. Finally, Component 6 was labelled 'fearful of conspecifics', and had high positive loadings on the traits fearful of conspecifics and aggressive to conspecifics. The trait friendly to conspecifics was negatively loaded onto this component.

6.3.3. Component scores

Females scored significantly higher than males on the components fearful-insecure (females: n = 47; $\overline{x}$ = 0.22 ± 0.1; males: n = 73; $\overline{x}$ = -0.13 ± 0.1; Mann-Whitney: U = 1248.0, $p<0.05$) and fearful of conspecifics (females: $\overline{x}$ = 0.46 ± 0.2; males: $\overline{x}$ = -0.29 ± 0.1; U = 1081.0, p = 0.001). Males scored higher than females on the component friendly to cheetahs, however this difference was found not to be significant.

Ratings were obtained for ten successful breeding pairs and 14 unsuccessful pairs. Comparison of the absolute differences of component scores within successful and unsuccessful breeding pairs revealed that individuals in unsuccessful breeding pairs were more similar to one another than individuals in pairs that had bred successfully (Figure 6.1). Mean absolute differences between individuals were higher in successful pairs than unsuccessful pairs across all components, indicating that the personalities of individuals in successful breeding pairs were more divergent than those of individuals in unsuccessful pairs. These differences between successful and unsuccessful pairs approached significance at the 5% level on two components: friendly to conspecifics (successful pairs: n =10; $\overline{x}$ = 1.01 ± 0.2; unsuccessful pairs: n = 14; $\overline{x}$ = 0.51 ± 0.1; U = 41.0, p = 0.096) and fearful of conspecifics (successful pairs: $\overline{x}$ = 1.02 ± 0.2; unsuccessful pairs: $\overline{x}$ = 0.57 ± 0.1; U = 38.0, p

= 0.064). However, the detection of significant differences was prevented by the small sample size. A post hoc power analysis, conducted using the program *G*Power 3* (Faul *et al*., 2007), revealed that the power of the tests to detect a large effect (*r* = 0.5: Chapter 5; Cohen, 1992) based on sample sizes of ten and 14 was 0.2; lower than the recommended level of 0.8 (Cohen, 1992; Field, 2013).

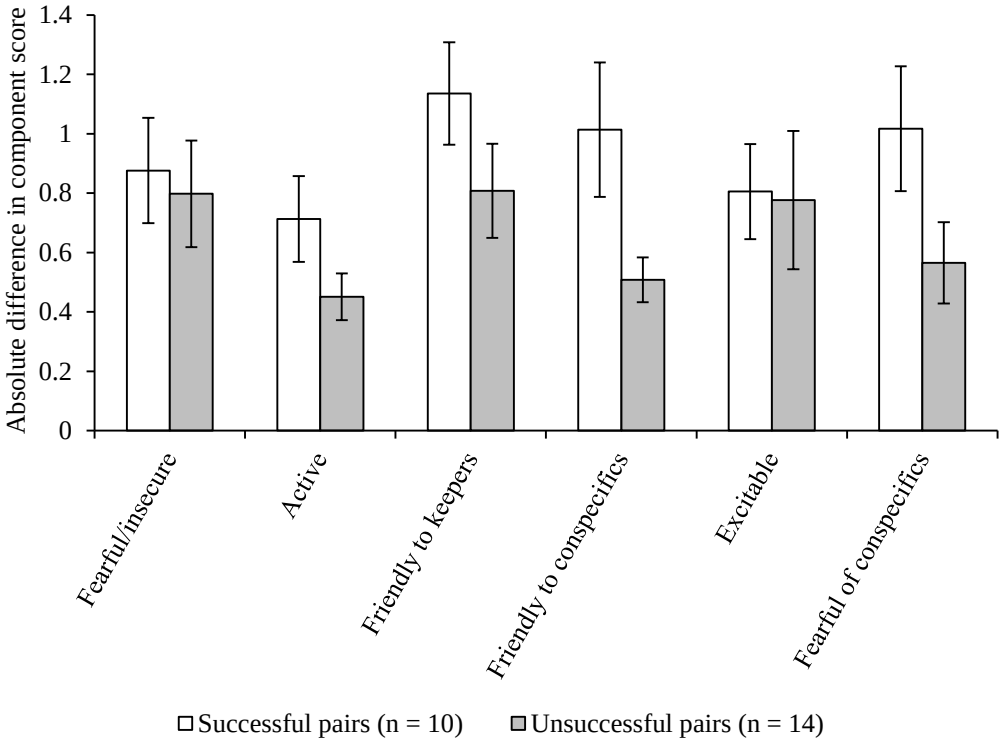

Figure 6.1. Mean absolute differences in component scores of successful and unsuccessful breeding pairs. Error bars represent the standard error of the mean.

Cheetahs housed in groups scored significantly higher than singly-housed cheetahs on the components friendly to keepers (group-housed: n = 35; $\overline{x}$ = 0.02 ± 0.1; singly-housed: n = 28; $\overline{x}$ = -0.47 ± 0.2; U = 324.0, p<0.05) and friendly to conspecifics (group-housed: $\overline{x}$ = 0.29 ± 0.1; singly-housed: $\overline{x}$ = -1.17 ± 0.2; U = 148.0, p<0.001). When males and females were analysed separately, further differences emerged in component scores between singly-housed

and group-housed individuals. Group-housed males scored higher than singly-housed males on friendly to keepers (group-housed males: n = 22; $\overline{x}$ = 0.08 ± 0.2; singly-housed males: n = 14; $\overline{x}$ = -0.58 ± 0.3; U = 85.0, p<0.05) and friendly to conspecifics (group-housed males: $\overline{x}$ = 0.46 ± 0.1; singly-housed males: $\overline{x}$ = -0.97 ± 0.4; U = 40.0, p<0.001). Group-housed males also had lower scores than single males on the component fearful of conspecifics (group-housed males: $\overline{x}$ = -0.83 ± 0.1; singly-housed males: $\overline{x}$ = -0.44 ± 0.2; U = 93.0, p<0.05). Similarly, group-housed females scored higher than singly-housed females on friendly to conspecifics (group-housed females: n = 13; $\overline{x}$ = 0.01 ± 0.2; singly-housed females: n = 14; $\overline{x}$ = -1.40 ± 0.4; U = 35.0, p<0.01), and they also had higher scores on the component excitable than singly-housed females (group-housed females: $\overline{x}$ = 0.40 ± 0.2; singly-housed females: $\overline{x}$ = -0.67 ± 0.2; U = 20.0, p<0.001).

There were significant differences between hand reared and parent reared individuals on two components. Hand reared cheetahs scored lower than parent reared cheetahs on the component fearful-insecure (hand reared: n = 17; $\overline{x}$ = -0.48 ± 0.2; parent reared: n = 98; $\overline{x}$ = 0.08 ± 0.1; U = 529.0, p<0.05). Scores on the component friendly to keepers were higher for hand reared individuals than parent reared individuals (hand reared: $\overline{x}$ = 1.18 ± 0.2; parent reared: $\overline{x}$ = -0.23 ± 0.1; U = 203.0, p<0.001).

6.4. Discussion

The objective of the research presented in this chapter was to explore the relationship between cheetah personality profiles, behaviour and reproductive success. It was hypothesised that keepers would be able to reliably rate cheetah personality, and that their ratings would be valid and related to behaviour. Reliability reached statistically acceptable thresholds and significant, positive correlations were found between behavioural observations and keeper ratings. Results therefore support this hypothesis.

Following the results of Wielebnowski's (1999) study, it was predicted that cheetahs that had not bred successfully would be rated as more fearful by their keepers. Results do not support this hypothesis. Although a 'fearful-insecure' component of cheetah personality was uncovered in the present research, no differences were found between the scores of breeders and non-breeders on this component.

Further, it was hypothesised that individuals housed in social groups would score highly on personality traits related to sociability (Murray, 1998; Kuhar *et al*., 2006). The component 'friendly to conspecifics' represented sociability and was characterised by positive loadings on the traits 'friendly to conspecifics' and 'playful', and negative loadings on the trait 'solitary'. Group-housed individuals scored significantly higher on this component than singly-housed individuals. Results therefore support this hypothesis.

This research is the first of its kind to collect personality ratings on a large sample of cheetahs (120 individuals) living in zoos throughout the EEP region and beyond. Inter-rater reliability was high, indicating that the keepers surveyed agreed with one another in their assessment of cheetah personality traits. Tests for inter-rater reliability did not always reach statistical significance, due to the small numbers of animals housed in each of the zoos. This is a common problem in zoo research, where small sample sizes can mean that tests are underpowered (Powell & Svoke, 2008). In the present research, zoos housed between one and 13 cheetahs and, as a result, reliability could not be statistically tested in some cases. Nonetheless, results of reliability analyses reached thresholds considered acceptable in previous peer-reviewed studies. In the study by Wielebnowski (1999), which the questionnaire used in the present research builds upon, values of Kendall's coefficient of concordance ranged from 0.57 to 0.98 on 15 of the 18 traits. Three traits with values of *W* below 0.5 were excluded from further analyses: friendly to people; friendly to conspecifics and solitary. In the present research, it was decided not to remove any traits because mean

values of *W* were greater than 0.5 for all traits, and overall mean values of *W* and r_s were greater than 0.6 (Pankhurst *et al*., 2009; Weiss *et al*., 2009).

To examine the validity of keeper ratings, direct observations of behaviour were correlated with trait scores for a sub-sample of 32 cheetahs. Several traits correlated significantly with behavioural observations, indicating that the ratings provided by the keepers reflected the behaviour shown by the animals. In particular, cheetahs rated as aggressive to conspecifics were recorded as showing higher rates of aggression towards other cheetahs. Animals that had been observed pacing were rated as eccentric (shows stereotypic or unusual behaviours) by their keepers, and those rated as more curious (approaches and explores changes in the environment) showed higher rates of exploratory behaviour.

As is the case in previous research, some personality traits did not correlate with any of the observed behaviours. Wielebnowski (1999) found no relationships between the traits eccentric, playful, smart and vocal and the responses of cheetahs to mirror-image stimulation. Similarly, Gartner and Powell (2012) compared personality ratings of snow leopards with their responses to novel objects. They found that the personality dimensions 'active/vigilant' and 'curious/playful' were positively correlated with the number of visits to the novel object and time spent performing exploratory behaviours. However, the dimensions 'calm/self-assured', 'friendly to humans' and 'timid/anxious' did not correlate with any observed behaviours. As Wielebnowski (1999) pointed out, trait rating questionnaires are designed to measure "attributes that escape conventional measurement" (Wielebnowski 1999, p. 344), and make use of keepers' aggregate knowledge of their animals that has been accumulated over time. It is not uncommon to find that some personality traits do not correlate with direct observations of behaviour. The results here are thus consistent with the expectation that agreement between ratings and behavioural measurements would be found on a subset of rated traits.

Exploratory factor analysis revealed six components of cheetah personality: fearful-insecure; active; friendly to keepers; friendly to conspecifics; excitable and fearful of conspecifics. Some of these components are analogous to those found in previous studies of felid personality. In their recent review of felid personality studies, Gartner and Weiss (2013a) found that felid personality had been previously described by up to eight dimensions, broadly defined as: 'sociable'; 'dominant'; 'curious'; 'active'; 'aggressive'; 'calm'; 'timid' and 'excitable'. The component friendly to conspecifics, found in the present research, can be considered as 'sociable', as the traits friendly to conspecifics and playful had high positive loadings on this component, and the trait solitary was negatively loaded onto this component. Similarly, Baker and Pullen (2013) also found a sociability dimension in cheetahs, with high positive loadings on the trait playful.

The component fearful-insecure can be considered similar to 'timid', with high positive loadings on the traits fearful of familiar people, fearful of unfamiliar people, insecure and tense, and a negative loading on the trait self-assured. This component is similar to the tense-fearful component found by Wielebnowski (1999), which also had positive loadings on the traits insecure, tense, fearful of conspecifics and fearful of people, as well as a negative loading on the trait self-assured. Gartner and Powell (2012) found a timid/anxious dimension in snow leopards, consisting of the traits anxious, fearful, insecure and tense.

The component 'active' was similar to the dominance dimension found in Scottish wildcats (Gartner & Weiss, 2013b), with positive loadings on the traits aggressive to conspecifics and active. This component also had similarities with a snow leopard dimension labelled 'active/vigilant' (Gartner & Powell, 2012).

In addition to the eight dimensions listed by Gartner and Weiss (2013a), a component labelled 'friendly to keepers' was uncovered in the present research. Baker and Pullen (2013) also found a similar component in their study of cheetahs, as did Gartner and Powell (2012) in

snow leopards. The importance of the keeper-animal relationship in zoo animal welfare has previously been highlighted. Mellen (1991) found that positive interactions with keepers increased the likelihood of breeding success in small felids, and the trait 'friendly to keeper' was negatively correlated with faecal corticoid concentration in white rhinos (Carlstead & Brown, 2005). Conversely, animals rated as fearful of people showed signs of poor welfare, such as elevated faecal corticoid concentrations (Carlstead, 2009). In the only published study to assess the personalities of both felids and their keepers, Phillips and Peck (2007) found that tiger keepers who were more neurotic had fewer interactions with their animals than keepers who were less neurotic. There were also some indications that the personality of the tigers influenced their interactions with the keepers, as an 'external awareness' trait was positively correlated with the number of approaches made towards the tigers by the keepers. However, the authors concluded that keeper personality had a greater influence on tiger-keeper interactions than did tiger personality (Phillips & Peck, 2007).

Despite the use of the same questionnaire and methods of data analysis as Wielebnowski (1999), different components were found in the present research. This may be due to the addition of two traits to the keeper questionnaire, to include information on cheetah's reactions to familiar and unfamiliar people. In addition, three traits were removed by Wielebnowski (1999) from further analyses because they were not reliably rated (friendly to people, friendly to conspecifics and solitary), whereas here all 20 traits were deemed to be reliably assessed and were included in the Principal Components Analysis.

Baker and Pullen (2013) and Gartner and Weiss (2013a) referred to the effects of slight changes in the traits or behaviours used in a personality assessment on the results of subsequent factor analyses. Nonetheless, although different studies use different methods for assessing felid personality, including different adjectives for describing traits and different names for the resulting components or dimensions, it would appear that some personality

traits replicate across several felid species. This suggests that the development of a single questionnaire to assess felid personality in the future could be useful. Indeed, Watters and Powell (2012) advocated the use of a single personality questionnaire across similar species. The development of the Hominoid Personality Questionnaire (HPQ), which has been used to investigate chimpanzee and orang-utan personality (King & Figueredo, 1997; Weiss *et al*., 2002; King *et al*., 2005; Pederson *et al*., 2005; Weiss *et al*., 2009), has shown that it is possible to use the same questionnaire to assess personality across species. Such questionnaires should be extensively validated to ensure that they accurately assess the fundamental personality traits of all of the intended species (Tetley & O'Hara, 2012; Watters & Powell, 2012). Potentially, sufficient evidence is now accumulated to warrant further investigation of a felid-wide personality questionnaire.

No significant differences were found between breeders and non-breeders on the component 'fearful-insecure', although breeders did score lower on this component than non-breeders. When males and females were analysed separately, breeding females scored lower on the component 'fearful of conspecifics' than non-breeding females, although this difference was also not significant. This is in contrast to the results of Wielebnowski's study (1999), in which non-breeders scored significantly higher on the component 'tense-fearful' than breeders. This may be due to the fact that cheetahs in the present sample did not score highly on this component in general: the mean score across all individuals was 0.004. Thus, cheetah keepers did not consider their animals to be tense, insecure or fearful overall in the present research. In a further study, McKay (2003) also failed to find personality differences in breeders and non-breeders, however this may have been due to the small number of breeders in her sample (two males and five females). Using a combination of ratings of adjectives and of observable behaviours, Baker and Pullen (2013) did not find a personality dimension analogous to the components 'tense-fearful' (Wielebnowski, 1999) or 'fearful-

insecure' among three components. However, definitions of all of the adjectives and behaviours used by Baker and Pullen (2013) to derive these components were not presented. It may be the case that fearfulness in cheetahs is not as reliable a predictor of reproductive success as first thought. Further research, using a consistent rating instrument, is required in order to fully understand this lack of replication of a fearfulness component across studies.

Within the sample of 120 individuals, ratings were obtained for ten successful breeding pairs and 14 unsuccessful breeding pairs. Comparison of the absolute differences in component scores revealed that individuals in unsuccessful breeding pairs were more similar to one another than individuals in pairs which had bred successfully. Few studies have investigated pair compatibility in zoo-housed species. In their study of black rhinoceros personality, Carlstead and colleagues (Carlstead, Mellen *et al*., 1999) found that males with low dominance scores and females with high dominance scores were more likely to have bred successfully. Upon further analysis, the authors found a significant, positive correlation between the breeding success of a pair (the number of offspring produced per year spent together) and the difference in dominance scores between the female and male. Thus, more successful breeding pairs were composed of a more dominant female relative to the male (Carlstead, Mellen *et al*., 1999).

Schuett *et al*. (2011) investigated personality and reproductive success in pairs of zebra finches. They found that pairs with similar personality profiles raised healthier chicks than those whose personality profiles did not match. These finches were more exploratory and aggressive. The authors suggested that the personality of a male might indicate his strengths as a parent, and that females may choose mates on this basis (Schuett *et al*., 2011). These findings appear to contrast those of Carlstead and her colleagues (Carlstead, Mellen *et al*., 1999), and indeed of the present research, that pairs with opposite personalities were more likely to successfully produce offspring. This may be due to differences in the socio-ecology

of the study species; since male cheetahs and rhinoceros have no involvement in parental care, it is likely that females use different characteristics to choose suitable mates.

Zoo professionals are often of the opinion that certain individuals are more compatible, which affects the success of breeding pairs (Carlstead, Mellen *et al*., 1999), and this anecdotal evidence has been given some empirical backing (Carlstead, Mellen *et al*., 1999; Schuett *et al*., 2011). In addition to genetic analysis, personality assessments could therefore be used to recommend behaviourally compatible breeding pairs and improve reproductive success in captive breeding programmes. Of course, personality ratings cannot override genetic considerations when recommendations for breeding pairs are made by studbook keepers, but they could give an indication of which pairings are likely to be successful. The issue of pair compatibility is an emerging topic in the field of animal personality research and further investigation is required before the effects of personality on the success of breeding pairs can be fully understood. Since there is little or no scope for experimentally manipulating pair compositions, zoo breeding records will be a valuable resource for retrospective investigations of pair compatibility.

Whilst zoo-based studies of pair compatibility are likely to remain retrospective, the finding that successful breeding pairs of cheetahs had more divergent personality profiles than unsuccessful pairs merits further investigation. Only a small number of the cheetahs in the present research had been introduced to one another for breeding. Thus, further research with larger numbers of successful and unsuccessful pairs is required before more definite conclusions can be drawn.

Group-housed cheetahs scored significantly higher on the component friendly to conspecifics than singly-housed cheetahs. This difference was also apparent when males and females were analysed separately. Group-housed individuals were rated as more likely to initiate contact with other cheetahs and engage in playful behaviours, and less likely to avoid

other individuals. Whilst it is possible that singly-housed cheetahs were rated highly on the trait solitary simply because they were housed alone, housing individuals in groups does not prevent them from avoiding other group members or engaging in fewer social interactions. Thus, it was possible for group-housed individuals to be rated as less playful or more solitary by their keepers.

This question of cause and effect was briefly addressed by Kuhar *et al*. (2006), who found that an 'understanding' personality factor was related to social group housing in captive gorillas. Male gorillas scoring highly on this factor were more likely to be housed in social groups, whilst solitary males had low understanding scores. Nonetheless, Kuhar *et al*. (2006) argued that personality assessments can be used to indicate which individuals might be suitable for social group housing, and those who may benefit from solitary housing. The solitary males in that study had been removed from social groups due to frequent instances of aggression, and successful introductions of juvenile males to silverbacks that had scored highly on the understanding factor were also reported (Kuhar *et al*., 2006).

Similarly, Murray (1998) found a relationship between sociability and social group size in captive chimpanzees. Chimpanzees in social groups consisting of seven or more individuals were more sociable and playful, whilst those housed in pairs or trios were more solitary. Murray suggested that this may be due to the increased number of available partners for social interactions. The study highlighted the importance of social group complexity in the behavioural development of young chimpanzees, and the role of personality in the provision of appropriate social conditions.

In the present research, group-housed males scored significantly lower on the component 'fearful of conspecifics' than singly-housed males. Although not significant, they also scored lower on the component 'fearful-insecure'. Previous research has indicated that the presence of familiar conspecifics can ameliorate the physiological and behavioural effects

of environmental stressors. Schaffner and Smith (2005) found that cortisol levels in an established pair of female captive Wied's marmosets were lower than in a newly formed pair following relocation. The established pair also spent more time in contact with one another in the weeks following relocation than the newly formed pair. Similarly, the finding in the present research that group-housed males were generally less fearful than singly-housed males provides further evidence for the potential welfare benefits of housing captive male cheetahs in social groups (also discussed in Section 4.5 of Chapter 4).

The only differences found between males and females were on the components 'fearful-insecure' and 'fearful of conspecifics', with females scoring higher than males on both components. Female cheetahs can therefore be considered more generally fearful than males. This result echoes the findings of Wielebnowski (1999); the females in that study also scored significantly higher than the males on the component 'tense-fearful'. Gender differences in fearfulness and stress have also been found in sheep (Vandenheede & Bouissou, 1993), chimpanzees (Buirski *et al*., 1978), dogs (Wilsson & Sundgren, 1997) and clouded leopards (Wielebnowski, Fletchall *et al*., 2002). It has been suggested that fear is an adaptive trait in females, related to their need to protect offspring, their increased vigilance and their avoidance of aggressive or dominant males (Buirski *et al*., 1978; Wielebnowski, 1999; Wielebnowski, Fletchall *et al*., 2002). This may well be the case in cheetahs, as wild females must raise their offspring alone under threat of predation (Laurenson *et al*., 1992; Wielebnowski, 1999).

Significant differences were found in the component scores of hand reared and parent reared individuals. Hand reared cheetahs scored significantly lower on the component 'fearful-insecure' than parent reared cheetahs. Wielebnowski (1999) also found that hand reared individuals scored lower than parent reared individuals on the components 'tense-fearful' and 'aggressive', although no significant differences were found in her study because

only six hand reared cheetahs were rated. This finding may have wider implications for hand reared individuals in captive breeding and reintroduction programmes. Personality can have consequences for fitness and survivorship, particularly with regard to boldness and fearfulness (Bremner-Harrison *et al*., 2004; Dingemanse & Réale, 2005; McDougall *et al*., 2006; Smith & Blumstein, 2008; Nicolaus *et al*., 2012). Captive-bred individuals that are less fearful may suffer reduced fitness in the event that they are released into the wild (Bremner-Harrison *et al*., 2004; McDougall *et al*., 2006). Indeed, Bremner-Harrison *et al*. (2004) found that 'bold' captive-bred swift foxes (*Vulpes velox*) were less likely to survive following reintroduction than fearful individuals. Of 16 foxes, five died during the first six months following release and those individuals had significantly higher boldness scores than surviving foxes. 'Bold' foxes moved further away from den sites and approached novel stimuli more closely than fearful individuals. Thus, they were less likely to avoid potentially dangerous situations (Bremner-Harrison *et al*., 2004). Whilst measures to reduce fearfulness can enhance captive animal welfare, care should also be taken to conserve natural behaviours that improve the prospects of survival for reintroduced individuals (Tetley & O'Hara, 2012).

Hand reared cheetahs scored significantly higher on the component 'friendly to keepers' than parent reared cheetahs. Similarly, Carlstead (2009) found that hand reared maned wolves scored significantly higher on a component named 'affinity to keepers' than their parent reared counterparts. Positive keeper-animal relationships are likely to reduce fearfulness and stress (Wielebnowski, Fletchall *et al*., 2002; Carlstead, 2009) and improve the welfare of captive animals (Hosey & Melfi, 2012). In addition, Mellen (1991) reported an association between keeper contact and reproductive success in small felids. She found that cats were more likely to reproduce successfully if their keepers spent time interacting with them. However, Mellen (1991) also emphasised the importance of balancing positive keeper-animal interactions with the retention of some element of fearfulness in captive wild animals.

Differences in the personalities of hand reared and parent reared individuals have also been documented in chimpanzees. Murray (1998) found that hand reared chimpanzees were more 'eccentric' than parent reared individuals, and thus more likely to show stereotypic or unusual behaviours. This finding highlighted the importance of early social experiences in the development of species-specific behaviours, and contradicted previous suggestions that early experiences need not be with conspecifics in order for species-specific behaviours to be learned.

There are limitations associated with the methodology used to address the research objective that is the subject of this chapter. First, there are limitations associated with the use of rating instruments to collect personality data from institutions in different countries. Cheetah personality questionnaires were sent to the participating zoos in English. Where translation from English into the keepers' native language was required, this was carried out by the main contact at the zoo on receipt of the questionnaires. This was the case at six of the 14 European institutions who responded. Therefore, it is possible that the meanings of some of the adjectives or the definitions of the adjectives may have changed during translation and there is no way of checking whether or not this occurred. The same problem arose in a study by King *et al*. (2005), in which chimpanzee personality was rated by French-speaking staff at a wildlife sanctuary using a French translation of the HPQ. Minor differences in personality structure between the sanctuary chimpanzees and animals that had been rated previously, using the English version of the HPQ, were apparent. The authors suggested that this may have been due to inconsistencies in the translated questionnaire, as no back-translation was carried out to check that the definitions of the adjectives provided in the English version of the questionnaire were the same as those provided in the French version (King *et al*., 2005).

In a later study, Weiss *et al*. (2009) translated the HPQ into Japanese and compared ratings obtained on chimpanzees at a sanctuary in Japan with those obtained in North

American zoos by King and Figueredo (1997). Unlike the French version of the questionnaire (King *et al*., 2005), the Japanese questionnaire was back-translated to correct inconsistencies. The ratings obtained by Weiss *et al*. (2009) were as reliable as those obtained by King and Figueredo (1997), and resulted in the same six personality dimensions, providing evidence that chimpanzee personality can be reliably assessed by raters of different cultures (Weiss *et al*., 2009). In future research, personality questionnaires should be translated and back-translated to check for inaccuracies in trait descriptions. Nonetheless, the reliability of the ratings obtained in the present research reached acceptable thresholds. This method of assessing animal personality using keeper ratings is well established and with proper consideration of the limitations, useful conclusions can be drawn from such an analysis.

Second, even though inter-rater reliability was good and comparisons with observed behaviours demonstrated validity, the research would be improved if the repeatability of the survey could be demonstrated. Previous studies of animal personality have found significant, positive correlations between the results of keeper ratings collected up to two years apart (Carlstead, Mellen *et al*., 1999; Uher & Asendorpf, 2008; Horback *et al*., 2013), and a repeat survey by Carlstead and her colleagues (Carlstead, Mellen *et al*., 1999) yielded the same relationships between personality, behaviour and breeding success in black rhinoceros as had been found in their original study. A repeat survey of cheetah keepers was not possible in the present research due to time constraints. However the repeatability of other animal personality studies provides further evidence of the reliability and validity of keeper ratings.

Third, there are limitations associated with the use of data collated by third parties. Some discrepancies between the information received on ARKS reports and the information published in the International Cheetah Studbook were discovered during this study. Where discrepancies arose, the data from the studbook were considered accurate. In addition, the studbook is published two years in arrears, so some of the data used in this study were not up

to date. It is possible that there are more successful breeders and more successful breeding pairs present in the current sample, but data on litters born after 2011 have not yet been published. These limitations are inherent in all studies using zoo records. However, with proper consideration of the constraints existing within the data set, useful conclusions can still be drawn.

6.5. Conclusion

The importance of individual differences has long been recognised in the study of animal welfare. Animals vary in their responses to the captive environment and consequently there is variation in the degree of well-being experienced by individuals. Research presented in this chapter has shown that cheetah keepers are able to reliably rate their animals on various personality traits, and their ratings are valid and related to behaviour. Personality was found to be related to gender and rearing history, and provided insight into the success of breeding pairs and social group cohesion.

Personality assessments can be used to provide insight into the subjective mental experiences, tendencies and dispositions of captive animals, and can inform important management decisions relevant to welfare. The assessment of personality, with careful application, is a potentially valuable tool for zoo professionals for improving the welfare of the animals in their care.

7. Discussion and conclusions

7.1. Introduction

In this chapter, I present a final discussion of the research contained in this thesis. The findings of each investigation into the stated objectives and hypotheses of the research are discussed, and the contribution of these findings to the body of knowledge on captive cheetah behaviour is considered. The limitations associated with the research are also discussed, along with the implications of the findings for captive cheetah management and recommendations for further research. The chapter ends with a list of the major conclusions drawn from the research.

7.2. Discussion

The research contained within this thesis utilised a number of approaches in order to determine the effects of social group housing and personality on the behaviour and reproductive success of captive cheetahs. The research addressed the following objectives:

1. To compare the behaviour and activity of captive cheetahs housed in natural and unnatural social group types.
2. To investigate spatial association in group-housed cheetahs.
3. To explore the relationship between cheetah personality profiles, behaviour and breeding success.

These objectives were addressed using a combination of behavioural observations, Geographic Information Systems (GIS) and keeper questionnaires. Previous research on social group behaviour in captive cheetahs is limited. This is surprising, given the problems encountered by zoological institutions in breeding the species and the complex social system

that has been observed in wild cheetahs. Previous studies investigating the reasons for the cheetah's poor reproductive performance in captivity concluded that it may be a result of some aspect of the captive environment. Wild and captive cheetahs share a lack of genetic diversity (O'Brien *et al*., 1985; Caro, 1993; Lindburg *et al*., 1993; Brown *et al*., 1996), however wild cheetahs show high rates of reproduction compared to the captive population (Laurenson *et al*., 1992; Marker, 2012c). In addition, no differences in reproductive physiology have been found between breeders and non-breeders of both sexes in the captive population (Wildt *et al*., 1983, 1987; Wielebnowski & Brown, 1998). Several authors therefore identified the need for further research into the behaviour and management of captive cheetahs (Laurenson *et al*., 1992; Caro, 1993; Lindburg *et al*., 1993; Wielebnowski, 1996; Wielebnowski & Brown, 1998; Wielebnowski, Ziegler *et al*., 2002; Crosier *et al*., 2007; Bauman *et al*., 2010), yet little effort had previously been made to investigate captive cheetah social behaviour in detail.

The present research addressed this gap in the literature. It collated information on cheetah behaviour, association and personality and provided quantitative evidence of the effects of social group housing on the behaviour of captive cheetahs. The main findings can be summarised as follows:

1. The type of social group in which captive cheetahs are housed can affect their behaviour. Cheetahs housed in unnatural social groups exhibited more pacing behaviour (typically associated with poor welfare) than cheetahs housed in natural social groups. Coalitions of males displayed the species-specific social behaviours that have been observed in their wild counterparts. Females, naturally solitary in the wild, can be safely housed in groups with few aggressive interactions. However, pacing behaviour observed in group-housed females suggests that housing females in groups should, if possible, be avoided.

2. A new method was devised for correcting observed indices of association to take into account chance encounters. Left uncorrected for, chance encounters can lead to spuriously high association indices. Indices of association calculated for all dyads were higher than those calculated using simulated chance encounters. Corrected indices of association were positively correlated with rates of affiliative interactions. Individuals were not only observed in proximity but also interacted with one another.
3. Relatedness is an important factor in captive cheetah social interaction. Related individuals groomed one another more than unrelated individuals and aggressive interactions were more frequent within unrelated dyads. Related individuals were also observed in close proximity more often than unrelated individuals.
4. The type of social group in which cheetahs are maintained can affect institutional reproductive success. Zoos housing their cheetahs in social groups that occur in wild populations produced more litters of cubs per year than those housing their cheetahs in unnatural-type groups.
5. In contrast to previous research, there were no differences in fearfulness between breeders and non-breeders. However, personality may be a predictor of pair compatibility and social group cohesion. Successful breeding pairs were composed of individuals with more divergent personalities than unsuccessful pairs and group-housed cheetahs were more sociable than singly-housed cheetahs.

Appropriate social group housing is important for captive animal welfare. Housing animals in appropriate social groups allows them the opportunity to express the species-specific social behaviours that have been observed in their wild counterparts (De Rouck *et al*., 2005; Price & Stoinski, 2007; Swaisgood & Schulte, 2010). This can also directly affect reproductive success (Mellen, 1991; Carlstead & Shepherdson, 1994; Kleiman, 1994; Lindburg & Fitch-Snyder, 1994; Wielebnowski, 1998), educate the public about interesting

species characteristics (Caro, 1993) and optimise the use of available accommodation. In contrast, inappropriate social groupings can have negative consequences for animal welfare, including increased social tension, aggression and chronic stress (Morgan & Tromborg, 2007; Price & Stoinski, 2007; Davis *et al*., 2009; Swaisgood & Schulte, 2010).

This research provides further evidence of the benefits of appropriate social group housing, and of the potential consequences of unnatural social groupings in captivity. Coalitions can be characterised by mutual tolerance, affiliative behaviour and the maintenance of close physical proximity (Olson & Blumstein, 2009), as observed in bottlenose dolphins (Connor *et al*., 1992) and African lions (Schaller, 1972). Group-housed male cheetahs maintained close proximity to one another and affiliative interactions, as previously recorded in coalitions of male cheetahs in the wild (Caro, 1994), were observed in captive coalitions. Aggression was rare among all-male groups, even at feeding times. In addition, pacing behaviour was less prevalent in cheetahs housed in natural-type groups than unnatural-type groups. Thus, the results provide quantitative evidence of the behavioural benefits of housing male cheetahs in coalitions in captivity.

Little evidence of social tension was observed in unnatural-type groups. Specifically, there were no differences in the rates of social interactions within natural and unnatural dyads. Group-housed females were observed in proximity more often than expected, with few instances of overt aggression and occasional affiliative interactions. Similar responses to enforced social proximity were observed by Dalerum *et al*. (2006) in captive wolverines (*Gulo gulo*). Social groupings of adults, other than mating pairs, are rare in this species, yet group-housed wolverines interacted with one another and aggression was infrequent. The authors suggested that this indicated greater flexibility in carnivore social systems than had previously been observed (Dalerum *et al*., 2006). However, in the present research, cheetahs housed in social groups that have not been observed in wild populations were more likely to

exhibit pacing behaviour than cheetahs housed in natural-type groups. Stereotypic pacing has been linked to physiological stress, including increased cortisol levels (Wielebnowski, Fletchall *et al*., 2002; Shepherdson *et al*., 2013), and is often observed in situations that result in poor welfare (Mason & Latham, 2004). Thus, housing captive cheetahs in groups that do not occur in wild populations should be avoided.

In addition to behavioural implications, results indicate that social group housing also affects reproductive success in captive cheetahs. Reproductive success was higher in institutions housing cheetahs in natural-type groups than unnatural-type groups. This may be the case for two reasons.

Firstly, housing males in groups may improve reproductive success in both sexes. It has been suggested that female reproductive activity is stimulated in the presence of a group of males (Brown *et al*., 1996; Wielebnowski & Brown, 1998). Most matings observed in the wild have occurred between females and coalition members (Caro, 1993) and ovulation in female cheetahs is often induced (Wildt *et al*., 1993; Caro, 1994; Brown *et al*., 1996; Wielebnowski & Brown, 1998; Wielebnowski, Ziegler *et al*., 2002). Housing males in groups increases the number of potential mates available to females, and could allow females the opportunity to choose between them. The importance of female mate choice has been documented in many mammalian species (Asa *et al*., 2011) and allowing some degree of mate choice can increase conception rates and offspring survival (Drickamer *et al*., 2000; Koeninger Ryan & Altmann, 2001; Anderson *et al*., 2007). Although mate choice in captive cheetahs has not been extensively studied, female cheetahs are able to distinguish between males according to genetic relatedness using olfactory cues (Mossotti, 2010). Providing access to multiple mates, rather than a single mate, is a possible strategy for implementing mate choice (Asa *et al*., 2011). Additionally, Ziegler-Meeks (2009) suggested that coalitions of males are better able to investigate a female's enclosure for signs of oestrus, and that males

in coalitions appear more “behaviourally confident” than single males (Ziegler-Meeks 2009, p. 26). This anecdotal evidence is supported by the finding that group-housed males were rated as less fearful by their keepers than singly-housed males. Thus, the presence of coalitions in captivity may be important for encouraging natural courtship behaviour in both males and females (Brown *et al*., 1996).

Secondly, it has been previously suggested that housing female cheetahs in pairs or groups can cause reproductive suppression (Brown *et al*., 1996; Jurke *et al*., 1997; Wielebnowski, Ziegler *et al*., 2002). The present research appears to support this contention. Whilst the results of behavioural observations and spatial analyses showed that it is safe to house compatible females in groups, zoos that did so between 2008 and 2011 did not produce any litters. The Association of Zoos and Aquariums (AZA) Husbandry Manual for the cheetah states that females recommended for breeding should be singly-housed (Ziegler-Meeks, 2009). This statement is supported by the present research. However, some group-housed females in the study displayed evidence of attachment, with higher rates of allogrooming and higher indices of association than expected. This may have welfare implications in the event that group-housed females are separated from their conspecifics (Tetley & O’Hara, 2013).

Social group cohesion may be influenced by the personalities of individuals. Results of the personality analysis revealed that group-housed cheetahs scored higher than singly-housed cheetahs on a ‘sociable’ personality component. The question of cause and effect has been raised previously in similar studies (Kuhar *et al*., 2006). It is possible that singly-housed cheetahs in the present research scored lower on this component and were rated as more solitary by their keepers simply because they were housed alone, with no opportunity to interact with conspecifics. However, behavioural observations validated the data collected from the keepers. Cheetahs housed in groups displayed affiliative behaviours including

allogrooming and social play, indicative of sociability, and observations of these behaviours were significantly correlated with keeper ratings of the relevant traits.

The effects of personality on social behaviour and group dynamics have been previously demonstrated in other species. Sapolsky and Share (2004) observed less aggressive behaviour in a troop of wild olive baboons following the deaths of aggressive males. The authors also noted reduced physiological stress in subordinate males, due to a decrease in unpredictable aggressive interactions. Kuhar *et al*. (2006) found that gorillas with high scores on an 'understanding' personality dimension initiated and received more affiliative behaviour and received less non-contact aggression than individuals with low understanding scores. In addition, Gartner and Weiss (2013b) described an 'agreeableness' personality dimension in Scottish wildcats. Individuals scoring highly on this dimension were rated as more co-operative, friendly to people and playful, and less fearful of both people and conspecifics. Given that personality dimensions relating to sociability have been uncovered in cheetahs by this and previous research (Chapter 6; Baker & Pullen, 2013), there is great potential for the use of personality assessments to predict which individuals might respond positively to social group housing (Kuhar *et al*., 2006; Gartner & Weiss, 2013b). This may be particularly relevant in the event that unrelated male cheetahs are introduced to one another to form coalitions consisting of related and unrelated individuals (Chadwick *et al*., 2013).

Preliminary evidence of pair compatibility in cheetahs was uncovered by this research. Mean absolute differences in component scores were higher for pairs that had bred successfully than for pairs that had not. Thus, the personality profiles of individuals in successful breeding pairs were more divergent than those of unsuccessful pairs. Previous research in this area is limited, with the majority of studies conducted on avian species (e.g. Schuett *et al*., 2011). In a similar analysis, Carlstead and her colleagues (Carlstead, Mellen *et al*., 1999) found that successful breeding pairs of black rhinoceros also had divergent

personalities, with successful pairs consisting of a dominant female and a submissive male. Due to the small number of paired individuals for whom personality ratings were received, the differences found in the present research were not statistically significant and this conclusion must be tentative. Nonetheless, the results present an interesting avenue of further investigation.

Although breeders scored lower on the component 'fearful-insecure' than non-breeders, and breeding females scored lower on the component 'fearful of conspecifics' than non-breeding females, this research did not find any significant differences in fearfulness between breeders and non-breeders. This is in contrast to the work of Wielebnowski (1999), who found that cheetahs scoring highly on the component 'tense-fearful' were less likely to have sired a litter. In a further study, McKay (2003) also failed to find personality differences between breeders and non-breeders, however this may have been due to the small number of breeders in her sample (two males and five females). Previous research has indicated a link between fearfulness and reduced reproductive success in other species. Powell *et al*. (2008) found that shy female pandas displayed fewer socio-sexual behaviours than females that were more confident or bold. Additionally, a meta-analysis of the fitness consequences of personality, carried out by Smith and Blumstein (2008) revealed that bolder individuals had increased reproductive success compared to more fearful individuals. In the present research, the mean score on the component 'fearful-insecure' was low; cheetah keepers did not consider their animals to be tense, fearful or insecure in general. It may be the case that fearfulness is not as reliable a predictor of reproductive success in cheetahs as first thought.

7.3. Limitations

The methods chosen to address the research objectives, while associated with a number of limitations, are appropriate for research of this type. Scan sampling and

instantaneous recording of behaviour provided an estimate of cheetah activity levels, and an all-occurrences recording method provided information on social interactions. The use of GIS enabled spatial association to be investigated in greater detail than has been achieved hitherto using similar techniques, and a trait rating method allowed information on cheetah personality to be collected on 120 cheetahs from 31 institutions. The limitations associated with each chosen method used in this research are discussed in the appropriate chapter, but are summarised below.

First, more field visits were made for behavioural observations during spring and summer months than during winter months. Whilst every effort was made to visit each zoo the same number of times and at different times throughout the year, field visits were constrained by time and the availability of funds (see Table 4.2, Chapter 4 for the schedule of field visits made). Ideally, field visits for behavioural observations would have been balanced across the year, with each zoo visited for the same length of time (see Table 4.1, Chapter 4 for the planned data collection schedule). Given that a significant relationship was found between temperature and activity (Chapter 4), there may be other seasonal variations in behaviour that were not detected in the present research. Within the constraints of this study the collection of more data was not feasible. Nonetheless, the number of observation hours in this study greatly exceeds previous studies of captive cheetah behaviour. Furthermore, no seasonal effects on reproduction are apparent in wild or captive cheetahs (Caro, 1994; Brown *et al*., 1996; Marker, Kraus *et al*., 2003; Augustus *et al*., 2006); consequently the conclusions of the present research are unaffected.

Second, it is acknowledged that digitising cheetah locations in the GIS from recordings made in the field can introduce errors into the analysis. The analysis relied on the accuracy of the digitised points, which in turn required accurate location recordings in the field. It is possible that the locations of the cheetahs in the exhibit and the locations recorded

onto the maps may have differed slightly, and it is not possible to retrospectively verify the locations. Potential errors in the location recordings were mitigated by observer experience and the lack of inter-observer variation. One other option would have been to remotely record location data using GPS devices; however the accuracy of available equipment and the need to anaesthetise individuals prevented the use of this technology. In addition, the simulation used to model chance encounters assumed equal use of the whole enclosure. Nonetheless, it provided an estimate of the effects of area and shape on the probability of a chance encounter and the introduction of this additional 'noise' in the data is unlikely to have had any marked effect on the results reported.

Third, there are limitations associated with the use of rating instruments to collect personality data from institutions in different countries. Cheetah personality questionnaires were sent to the participating zoos in English. Where translation from English into the keepers' native language was required, this was carried out by the main contact at the zoo on receipt of the questionnaires. Therefore, it is possible that the meanings of some of the adjectives, or of the definitions of the adjectives, may have changed during translation and there is no way of checking whether or not this occurred. However, the reliability of the ratings obtained in the present research reached acceptable thresholds and previous studies provided evidence that animal personality can be reliably assessed by raters of different cultures (Weiss *et al*., 2009). The method of assessing animal personality using keeper ratings is well established and with proper consideration of the limitations, useful conclusions can be drawn from such an analysis.

7.4. Recommendations

The research presented in this thesis has a range of potential applications. The simulation developed in Chapter 5 of the thesis, and the resulting probability table (Appendix

2), are useful tools for researchers studying association in both wild and captive animals (Chadwick *et al*., under review). Studies using indices of association should take into account chance encounters. The probability table can be used to determine whether or not chance encounters are of concern, and the simulation can be used to model chance encounters in any area. Furthermore, the results of the simulation can be used to correct indices of association. This is a novel method of calculating indices which excludes the effect of chance encounters (Chadwick *et al*., under review). The investigations into captive cheetah social behaviour and personality provided information which could be useful for captive cheetah care providers, and a basis for future research activities. A number of recommendations for future research and the management of captive cheetahs have arisen from the present research.

7.4.1. Recommendations to zoos

Captive cheetahs should be maintained in the social groups that occur in wild populations. Sibling males should be housed together and unrelated males can be introduced to siblings to form coalitions of three or four individuals before they reach 2 years of age (Chadwick *et al*., 2013). In light of the findings of this research, it would be beneficial to singly-house all breeding females following separation from their littermates at around 2 years of age. This would mirror the dispersal of litters of cubs in the wild (Caro, 1994). If space is limited, compatible females can be safely housed together with little aggression, with females recommended for breeding subsequently separated. However, such separation of females from their conspecifics may have welfare implications. Evidence of attachment between related females was observed in this research, as previously documented in males (Ruiz-Miranda *et al*., 1998; Tetley & O'Hara, 2013). Similarly, Lyons *et al*. (1997) observed pacing behaviour in a mixed-sex cheetah pair following separation, which ceased when the animals were reunited. This might also indicate a degree of attachment. Females prevented

from breeding at the request of the studbook keeper (e.g. Nina at Exmoor Zoo) can be housed with compatible conspecifics. Although few aggressive interactions were observed in the present research, careful monitoring of the behaviour of individuals remains a necessary precaution, as the response of animals to introductions into new groups cannot be easily predicted.

Despite the low rates of aggression observed among group-housed females, the potential welfare implications of unnatural social groupings highlighted by this research should not be ignored. Pacing behaviour has been linked with elevated cortisol levels, and may indicate chronic stress and poor welfare (Wielebnowski, Fletchall *et al*., 2002; Mason & Latham, 2004; Shepherdson *et al*., 2013). Thus, in the event that cheetahs are housed in unnatural-type groups, their behaviour should be monitored. Jurke *et al*. (1997) suggested that the presence of conspecifics may be a source of chronic stress in female cheetahs but were unable to investigate the effects of changes in social groupings due to space restrictions. Wielebnowski and colleagues also observed pacing behaviour in group-housed females, as well as long periods of anoestrus (Wielebnowski, Ziegler *et al*., 2002). The present research did not incorporate any hormone analyses which, coupled with behavioural observations, could provide more detailed information about the welfare state of individuals housed in unnatural-type groups. Such analyses would be useful to investigate the physiological effects of unnatural social groupings not only in females, but also in males.

Zoos should endeavour to include personality profiles within standard record keeping practices. The use of personality assessment to complement existing zoo record keeping techniques has recently been advocated by several authors (Whitham & Wielebnowski, 2009, 2013; Tetley & O'Hara, 2012; Watters & Powell, 2012), and the present research provides further evidence of the potential benefits of this practice. Cheetah keepers were able to reliably rate their animals on personality traits, and their ratings correlated with behavioural

observations. Understanding individual differences in personality in species that are prone to reproductive problems in captivity might make clear the reasons why certain individuals do not fulfil their reproductive potential. In addition, this may lead to improvements in the captive environment for those species (Powell *et al.*, 2008). Personality profiles could also provide an indication of how an animal might react to events such as transfers between collections and introduction into new social groups. Socially housed species could therefore benefit from personality assessments, as social group cohesion could be improved if the personalities of individuals to be housed together are known. Consequently, information about the personality of an individual could be invaluable to staff at institutions involved in co-ordinated captive breeding programmes.

7.4.2. Suggestions for further research

The present research uncovered a link between social group housing and institutional reproductive success. Further research on institutional reproductive success based on the types of social groups they maintain would be advantageous. This could take the form of a survey of social group types, coupled with information from zoo breeding records, and should include the collection of information from a larger number of institutions than was possible in the present research. If further research confirmed these results, it would provide compelling evidence for captive cheetah managers to adopt the recommendations for social group housing outlined above.

The application of GIS to the study of zoo animal behaviour has been demonstrated by this research. There is scope for further research on social proximity and enclosure use in zoo animals using the techniques advanced here. In particular, location data within a GIS could be used to track animal movements around exhibits, and provide information on which areas of an exhibit are most used by animals. Location data could also be analysed alongside

behavioural observations in order to investigate which activities are carried out by animals in particular areas of an exhibit. For example, in the present research, clusters of location points occurred in elevated areas in the enclosures, indicating a preference of cheetahs for high ground. Previous research has documented the use of elevated areas by captive felids for resting and vigilance (Lyons *et al*., 1997), as well as pacing behaviour around the edges of exhibits (Lyons *et al*., 1997; Mallapur *et al*., 2002). Knowledge of how animals make use of available exhibit space can inform future enclosure design and resource distribution within exhibits.

Preliminary evidence for pair compatibility in cheetahs was uncovered in the present research. However, further research is required in this area before robust conclusions can be drawn. This would require the assessment of the personalities of a larger proportion of the captive cheetah population than was achieved by the present research, in order to incorporate more individuals that have been placed together for breeding.

If zoos are to be successful in their aim of conserving vulnerable species, the behaviours that are specific to those species must also be conserved (Markowitz, 1997). Whilst encouraging reproduction is vital to the success of captive breeding programmes, care must be taken to avoid selection for traits that will be disadvantageous to those individuals should they be released into the wild (McDougall *et al*., 2006). In addition, zoo animals are central to the educational role of the modern zoo and the behaviour and personality of animals may affect the perceptions of zoo visitors (Caro, 1993; Melfi *et al*., 2004; Miller, 2012; Watters & Powell, 2012). Since variation in personality exists in wild populations (Dingemanse & Réale, 2005), maintaining variation in the captive population is integral to the success of captive breeding programmes. The effects of changes in personality due to selection in captivity remain largely unknown and further research in this area is required (Dingemanse & Réale, 2005; McDougall *et al*., 2006). Given that personality is heritable, the

systematic monitoring of zoo animal personality in multiple institutions could be used to track changes in personality due to captive breeding through the generations, to assist the retention of natural behavioural characteristics and further our understanding of artificial selection in captive breeding.

In order for personality assessments to be successfully implemented across multiple collections, as recommended above, there is a need for standardised keeper questionnaires to be devised for more zoo-housed species. Here, the term 'standardised' is used to denote a personality questionnaire for a specific species, that can be distributed to all collections holding that species. Reliability data must be obtained and researchers should report all aspects of their reliability analyses, including test results and rater numbers. Questionnaires must also be validated by comparing the results to other measures, such as behavioural observations. Information from personality assessments could then be shared between collections, with the knowledge that the assessment has been carried out using the same rating instrument for all the individuals. Thus, the development of standardised questionnaires will allow the results of personality assessments to be comparable between institutions and used alongside current animal record keeping systems.

Questionnaire development will require much research in the first instance. However, once a personality questionnaire has been validated for a particular species, many researchers and zoo professionals can benefit from it (Meagher, 2009; Whitham & Wielebnowski, 2009). To make the research process more efficient, Watters and Powell (2012) suggested that questionnaires be developed at the level of family, rather than species, to which items could be added as required by individual researchers. Indeed, the development of the Hominoid Personality Questionnaire (HPQ), which has been used to investigate chimpanzee and orang-utan personality (King & Figueredo, 1997; Weiss *et al*., 2002, 2009; King *et al*., 2005; Pederson *et al*., 2005), has shown that it is possible to use the same questionnaire to

investigate personality across species. Given that similar components of cheetah personality were found in the present research that have been described in previous studies of cheetahs – and indeed other felids – there is scope for the development of a felid equivalent of the HPQ. Such a questionnaire should be extensively validated to ensure that it accurately represents the fundamental personality traits of all the intended species covered.

7.5. Conclusions

This research has provided the first quantitative evidence of the effects of social group housing on captive cheetah behaviour, produced a method for correcting indices of association, and uncovered preliminary evidence of pair compatibility in cheetahs. The following conclusions can be drawn from the research:

1. The natural social groupings of wild male cheetahs can be replicated in captivity. Siblings can be successfully housed in coalitions and unrelated individuals can be introduced to siblings to form groups of three or four. Whilst housing females in groups did not result in overt aggression, group-housing of females should be avoided as it might lead to chronic stress and reproductive suppression.
2. Studies of social behaviour using an index of association should take into account chance encounters. Corrected indices of association showed that relatedness is an important factor in captive cheetah social interactions, with higher association indices between related than unrelated dyads. The methods developed in this research can be used to estimate the likely effect of chance encounters on association indices.
3. Social group housing and personality can affect captive cheetah reproductive success. The personality profiles of individuals in successful breeding pairs were more divergent than those of individuals in unsuccessful pairs. Furthermore, zoos housing their cheetahs in groups that do not occur in wild populations did not produce any

litters between 2008 and 2011. However, small sample sizes prevented the detection of statistically significant differences. Further research is required before robust conclusions can be drawn.

The goal of a successful captive breeding programme is a self-sustaining, genetically diverse population. Despite continued breeding efforts, this has not yet been achieved for the cheetah. This research has uncovered some of the factors which may contribute to the poor reproductive success of the captive cheetah population. It has demonstrated the importance of appropriate social group housing and highlighted the welfare benefits of maintaining captive cheetahs in the social groups that have been observed in wild populations. This thesis provides important information on an area of cheetah behaviour that has not previously been addressed. It is the first corpus of research to collate information on the behaviour of captive cheetahs housed in a range of social groups, and investigate links between social behaviour, personality and reproductive success. In addition, a new method was developed for calculating chance encounters and correcting indices of association. This made association indices for dyads in different exhibits directly comparable, and allowed the spatial aspect of captive cheetah social behaviour to be investigated in detail in a number of zoological institutions. It is hoped that the recommendations for conservation management improvements and further investigation offered by this research will assist captive cheetah care providers in achieving a self-sustaining population, capable of contributing to the conservation of this vulnerable species.

8. References

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Appendix 1

Example check sheet used to record behavioural observations.

Location _____ Enclosure _____ Date _____ Start Time _____ Observation session no. _____

Weather _____

Feed	Loc	Pace	Stand	Stand alert	Agg	Allo groom	Vocal	Soc play	Play	Scent mark	Sniff	U/D	Lie flat out	Lie out	Lie alert	Sit	Sit alert	Grm	Other	In house	O/S	Notes

Appendix 2

Probability of a chance encounter within a dyad in areas ranging from 20 units^2 to 10,000 units^2, with distance criteria of between 1 and 25 units. Shaded cells indicate probabilities of less than 0.05. Bold type indicates an effect of shape on the probability of a chance encounter; consequently these values apply only to squares.

Note: Due to rounding, values of less than 0.0005 are represented as zero and values greater than 0.9995 are represented as 1.

	Distance defining an association (units)																
Area (units^2)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	20	25
20	0.129	**0.408**	**0.711**	**0.925**	**0.994**	**1.000**	-	-	-	-	-	-	-	-	-	-	-
30	0.089	0.299	**0.550**	**0.778**	**0.936**	**0.992**	**1.000**	-	-	-	-	-	-	-	-	-	-
40	0.068	0.235	0.447	**0.663**	**0.841**	**0.955**	**0.993**	**1.000**	-	-	-	-	-	-	-	-	-
50	0.056	0.194	0.378	0.575	**0.754**	**0.893**	**0.972**	**0.995**	**1.000**	-	-	-	-	-	-	-	-
100	0.029	0.105	0.213	0.347	0.482	0.621	0.745	0.849	**0.928**	**0.975**	**0.993**	**0.998**	**1.000**	-	-	-	-
200	0.015	0.055	0.118	0.195	0.282	0.379	0.477	0.576	0.667	0.753	0.831	0.893	0.941	0.972	0.987	-	-
400	0.008	0.029	0.061	0.104	0.157	0.214	0.278	0.344	0.414	0.484	0.555	0.621	0.685	0.745	0.801	0.975	0.999
600	0.005	0.019	0.042	0.072	0.109	0.151	0.197	0.247	0.300	0.356	0.413	0.467	0.525	0.582	0.637	0.865	0.980
800	0.004	0.015	0.032	0.055	0.084	0.117	0.154	0.194	0.237	0.283	0.328	0.376	0.425	0.477	0.525	0.753	0.917
1000	0.003	0.012	0.026	0.045	0.068	0.096	0.126	0.160	0.196	0.236	0.275	0.317	0.360	0.405	0.447	0.663	0.842
1500	0.002	0.008	0.018	0.031	0.047	0.066	0.087	0.112	0.137	0.165	0.197	0.228	0.260	0.294	0.328	0.508	0.678
2000	0.002	0.006	0.013	0.024	0.036	0.050	0.067	0.087	0.107	0.128	0.153	0.177	0.203	0.231	0.258	0.410	0.564
2500	0.001	0.005	0.010	0.019	0.029	0.040	0.055	0.070	0.087	0.105	0.124	0.146	0.168	0.189	0.214	0.345	0.482
3000	0.001	0.004	0.009	0.016	0.024	0.034	0.046	0.058	0.075	0.089	0.105	0.124	0.144	0.162	0.183	0.298	0.423
3500	0.001	0.003	0.008	0.014	0.021	0.029	0.040	0.050	0.064	0.078	0.092	0.107	0.125	0.142	0.161	0.261	0.375
4000	0.001	0.003	0.007	0.012	0.018	0.026	0.035	0.045	0.056	0.069	0.082	0.096	0.110	0.127	0.142	0.234	0.339
4500	0.001	0.003	0.006	0.011	0.017	0.025	0.033	0.043	0.053	0.065	0.077	0.091	0.106	0.120	0.134	0.224	0.323
5000	0.001	0.003	0.005	0.010	0.015	0.020	0.028	0.036	0.046	0.055	0.066	0.078	0.090	0.105	0.117	0.194	0.282
5500	0.001	0.002	0.005	0.009	0.013	0.019	0.026	0.033	0.042	0.051	0.062	0.071	0.083	0.094	0.107	0.178	0.261
6000	0.000	0.002	0.004	0.008	0.012	0.017	0.024	0.030	0.038	0.047	0.056	0.066	0.077	0.087	0.099	0.165	0.244
6500	0.000	0.002	0.004	0.007	0.011	0.017	0.022	0.029	0.035	0.043	0.052	0.060	0.071	0.082	0.092	0.154	0.227
7000	0.000	0.002	0.004	0.007	0.011	0.015	0.020	0.027	0.033	0.040	0.048	0.058	0.066	0.076	0.087	0.144	0.214
7500	0.000	0.002	0.003	0.006	0.010	0.014	0.019	0.026	0.031	0.038	0.045	0.053	0.062	0.072	0.082	0.136	0.200
8000	0.000	0.001	0.003	0.006	0.010	0.013	0.018	0.023	0.029	0.036	0.043	0.051	0.058	0.068	0.076	0.129	0.190
8500	0.000	0.001	0.003	0.005	0.008	0.013	0.017	0.022	0.027	0.033	0.041	0.048	0.055	0.063	0.072	0.121	0.180
9000	0.000	0.001	0.003	0.005	0.008	0.012	0.016	0.021	0.027	0.032	0.039	0.044	0.053	0.059	0.069	0.117	0.173
10000	0.000	0.001	0.003	0.005	0.008	0.011	0.015	0.018	0.024	0.030	0.034	0.041	0.048	0.055	0.061	0.106	0.156

Appendix 3

Cheetah personality questionnaire. Adapted from Wielebnowski (1999).

RATING INDIVIDUAL CHEETAHS

Procedure:

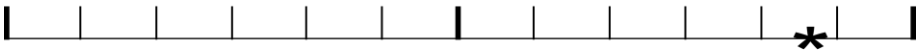
Please rate each individual on the continuous scale provided for each adjective (20 adjectives). The names of the individuals are all listed on one sheet per adjective to allow you to evaluate each individual relative to the others. Please do not discuss your answers with anyone else.

EXAMPLE:

ACTIVE

Moves around enclosure (e.g. paces, runs, stalks)

Not at all Somewhat A lot



Individual X

A separate comment sheet is provided to allow you to add information not covered by the adjectives for each individual. Please include any additional adjectives you can think of in your comments. Comments should also include how each individual usually reacts to you specifically.

Please provide the following information about yourself below:

Name: Date:

Sex: F M

Number of years worked with cheetahs overall:

Number of years worked with cheetahs at this institution:

Number of years worked with the current group of cheetahs:

Average number of hours per week spent with the cheetahs:

Do you routinely enter the enclosure with the cheetahs?

Number of years worked with animals in general:

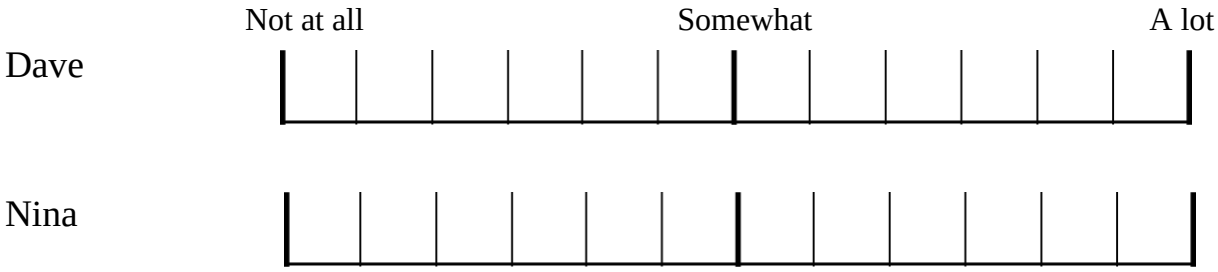
Do you particularly like cheetahs or cats in general? (e.g. Are you a “dog” or a “cat” person?)

Do you believe that there are distinct personalities among your cheetahs?

Do you feel that certain personality differences could be correlated with reproductive success? Disease? How the individual copes with stress?

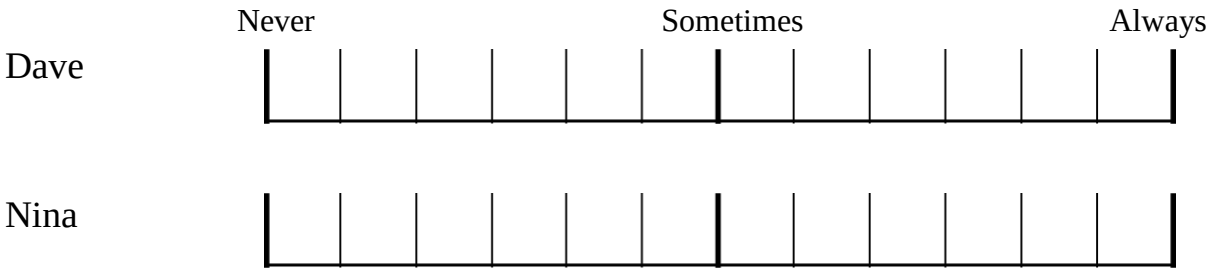
ACTIVE

Moves around enclosure (e.g. paces, runs, stalks)



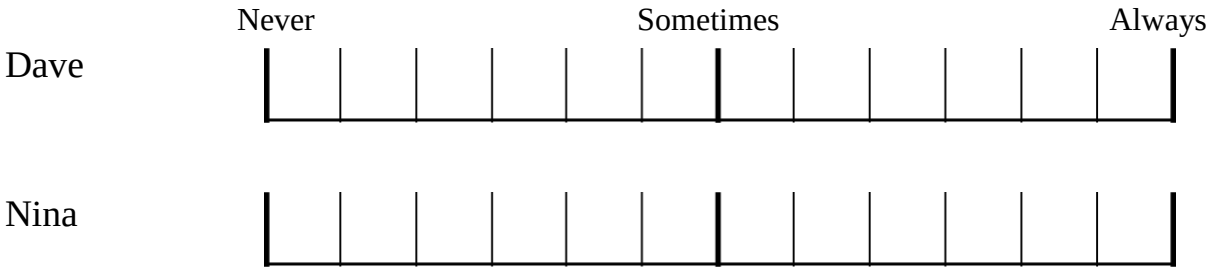
AGGRESSIVE TO CONSPECIFICS

Reacts hostile (e.g., attacks, growls) towards other cheetahs



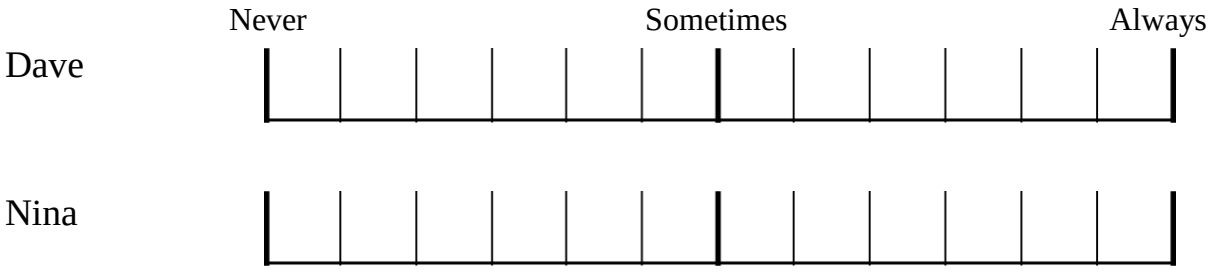
AGGRESSIVE TO FAMILIAR PEOPLE

Reacts hostile and threatening towards familiar keepers and staff members



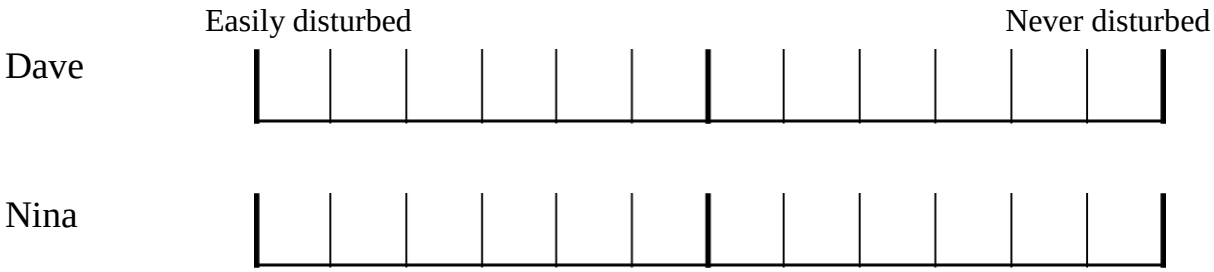
AGGRESSIVE TO UNFAMILIAR PEOPLE

Reacts hostile and threatening towards unfamiliar staff and members of the public



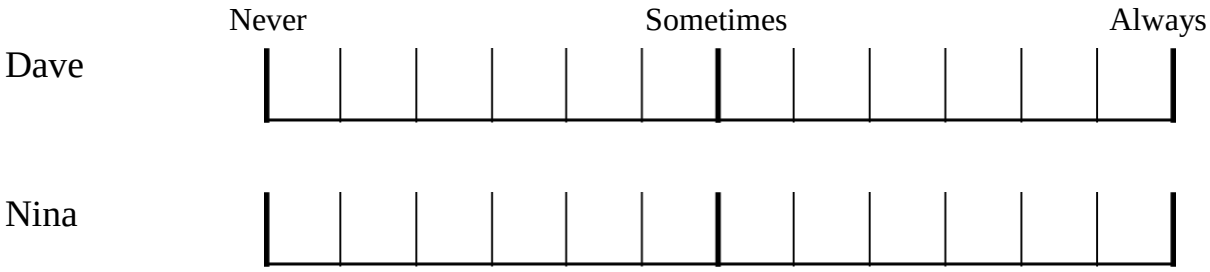
CALM

Not easily disturbed by changes in the environment



CURIOUS

Approaches and explores changes in the environment

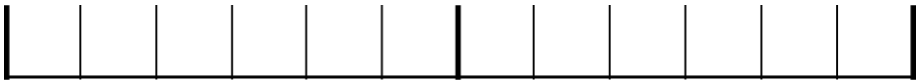


ECCENTRIC

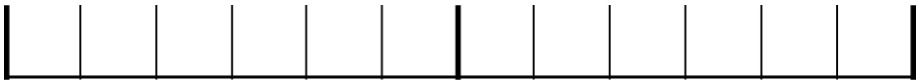
Shows stereotypic or unusual behaviours

Never Sometimes Always

Dave



Nina

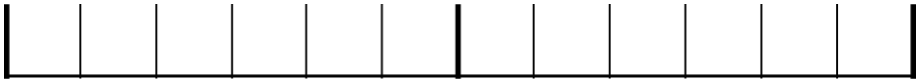


EXCITABLE

Overreacts to changes in the environment

Never Sometimes Always

Dave



Nina

FRIENDLY TO CONSPECIFICS

Initiates and seems to seek proximity of other cheetahs

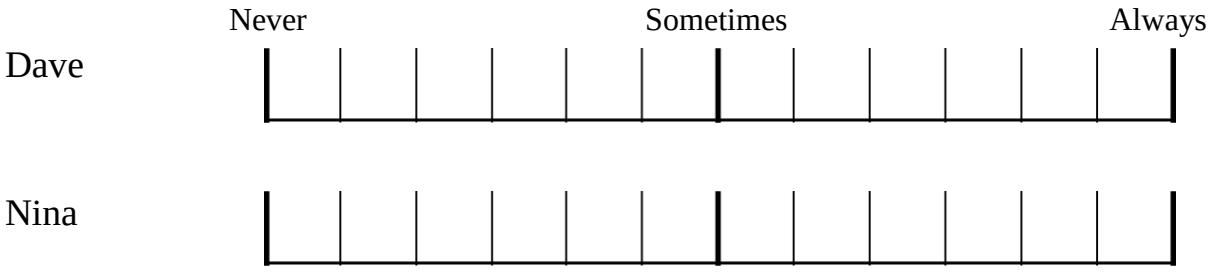
Never Sometimes Always

Dave

Nina

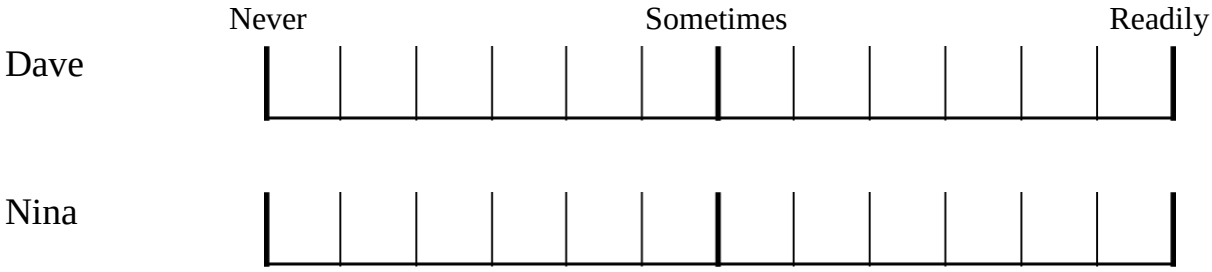
FRIENDLY TO KEEPERS

Initiates proximity with keepers; approaches fence readily and in a friendly manner (e.g. purrs, rubs on fence)



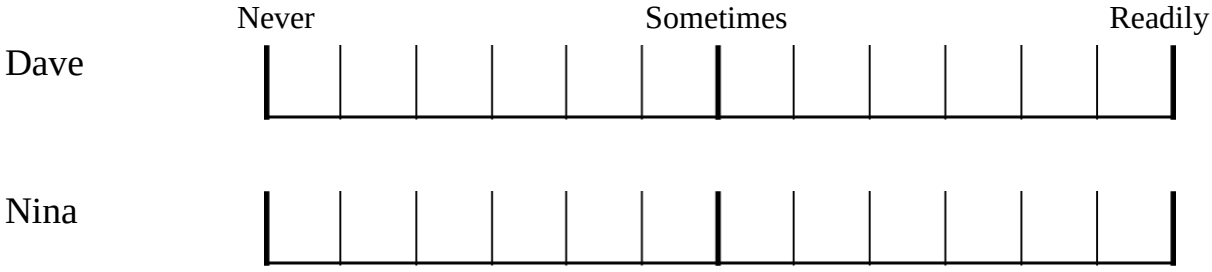
FEARFUL OF CONSPECIFICS

Retreats and hides from other cheetahs



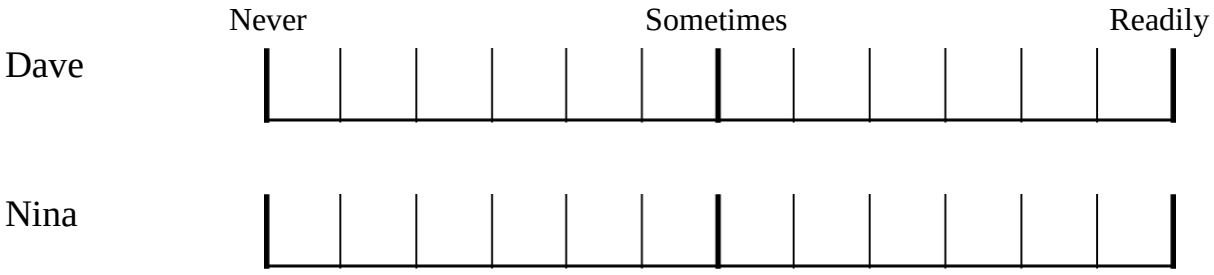
FEARFUL OF FAMILIAR PEOPLE

Retreats and hides from familiar keepers and staff members



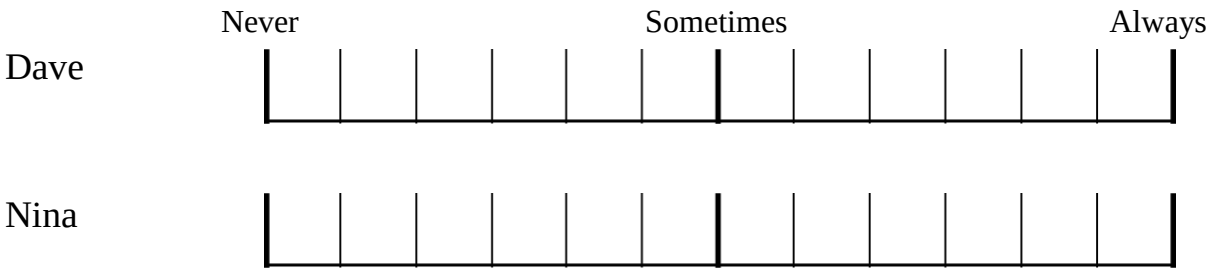
FEARFUL OF UNFAMILIAR PEOPLE

Retreats and hides from unfamiliar staff and members of the public



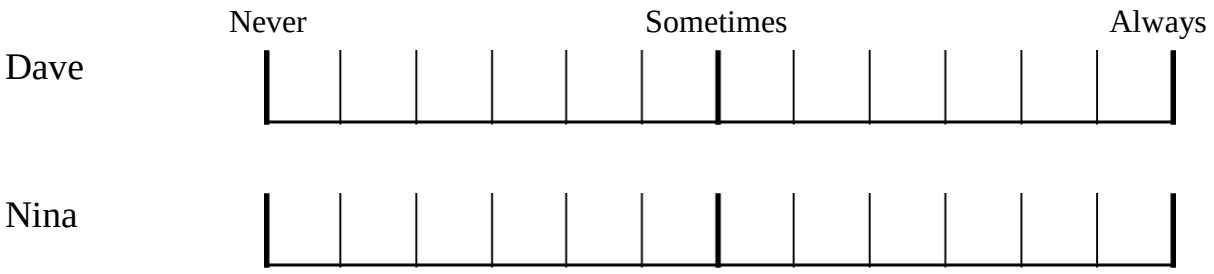
INSECURE

Seems scared easily; "jumpy" and fearful in general



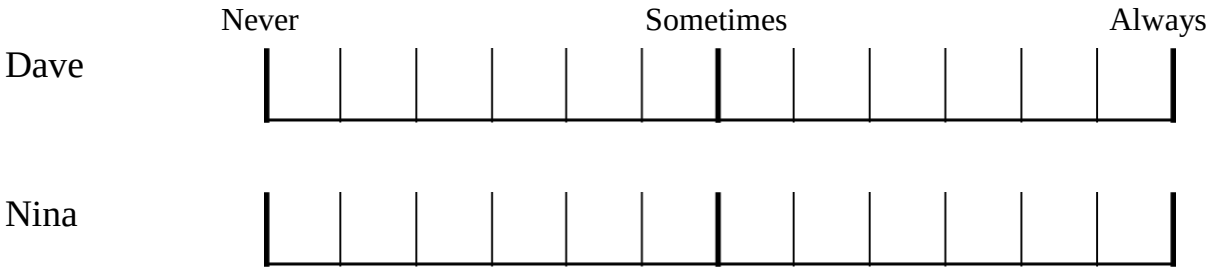
PLAYFUL

Initiates and engages in play behaviour (seemingly meaningless, non-aggressive behaviour) with objects and/or other cheetahs



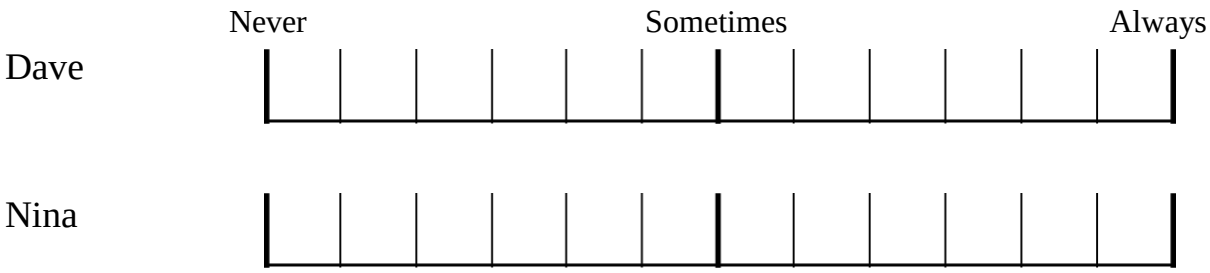
SELF-ASSURED

Moves in a seemingly confident, well-co-ordinated and relaxed manner



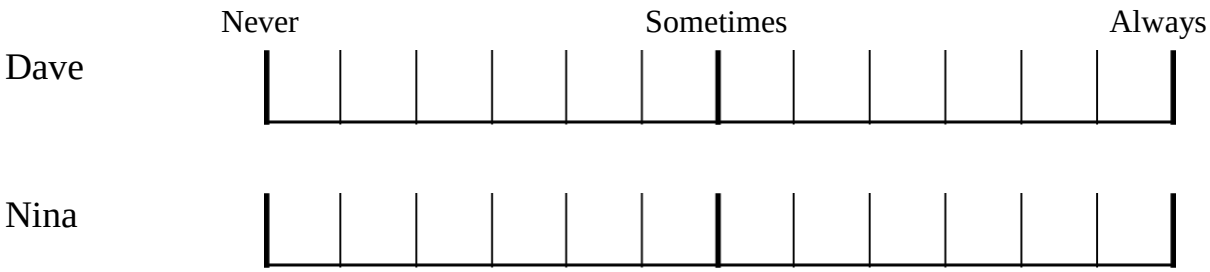
SMART

Learns quickly to associate certain events and appears to remember for a long time



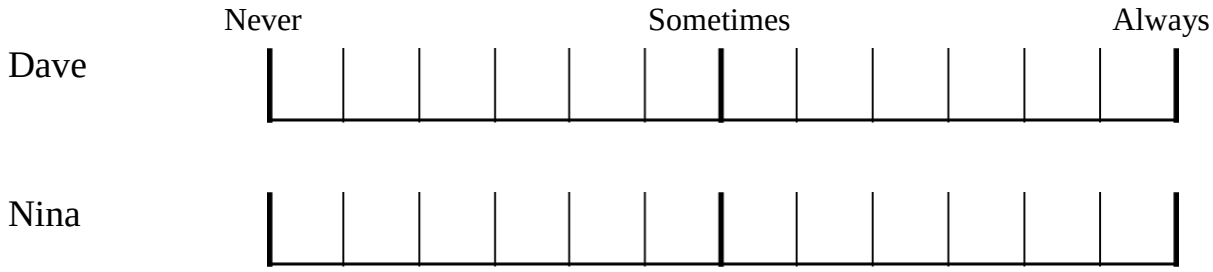
SOLITARY

Spends time alone; avoids company



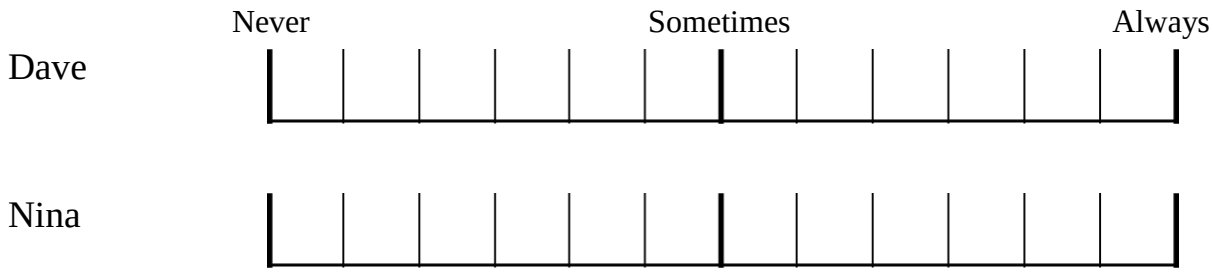
TENSE

Shows restraint in movement and posture



VOCAL

Frequently and readily vocalizes



COMMENTS

Dave:

Nina: